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Taxonomy and ecology of Cretaceous Cassiopidae (Mesogastropoda)

R. J. Cleevely and N. J. Morris

Dept. of Palaeontology, British Museum (Natural History), Cromwell Road, London SW7 5BD

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Synopsis

The family Cassiopidae is defined and its characteristics and probable relationships discussed; the nomenclature of several higher taxa within the family is examined and stabilized. The type species of the genera *Cassiope* and *Paraglauconia* are verified and described.

Seven species of British Lower Cretaceous Cassiopidae (Mesogastropoda, Cerithiacea?) are redescribed and figured: *Gymnentome pizcuetana, Paraglauconia tricarinata, P. lujani, P. fittoni, P. shipbornensis, Mesoglauconia arkelli, M. renevieri*. Their generic assignments are examined and the significance of their stratigraphical occurrence established.

The geological history of the family is reviewed. By comparison with the ecology of Recent Cerithiacea, the evidence of associated faunas indicates a probable marine estuarine or mangal-like habitat for the Cassiopidae. The European palaeogeographical distribution of the family is briefly considered.

Introduction

The occurrence of the Cassiopidae is readily accepted as an indicator of a particular ecological environment. They are relatively common in intertidal environments of Pan-Tethyan, or 'non-boreal', Cretaceous deposits. Akopyan (1976: 131) believed that their distribution, although relatively widespread, was facies controlled. As discussed below (p. 274) brackish water affinities have been attributed to them (Casey 1961: 516), but examination of their faunal associations has established that the majority are marine (Simpson 1983; Mennessier 1984 : 102; Cleevely *et al.* 1984; Kase 1984: 119). According to Morter (1984), the cassiopids form part of one of the typical molluscan associations occurring during the periodic marine incursions of the Weald and Wessex Basins during the Lower Cretaceous. Their frequent association with lignitiferous deposits (see Coquand, 1865; Aguiular *et al.* 1971) has led Mennessier to argue that such deposits might well indicate the proximity of a mangrove environment. Our interpretation (Cleevely *et al.* 1984) of the Lower Cretaceous Punfield Marine Band fauna of Dorset (and of a flora that provides no evidence of mangrove species; p. 102) is that it is from an estuarine or in-shore situation. Mennessier also postulated that it was their lower oxygen requirements (i.e. lower than those of other gastropods of a comparable size) that had enabled the cassiopids to exploit such habitats, rather than any difference in their salinity tolerances.

The description of these turriculate-conical gastropods, in which ornament is extremely variable, has resulted in considerable taxonomic confusion, largely because of their division into innummerable species which have then frequently been misinterpreted. The work of Akopyan (1976) on the rich, well-preserved late Cretaceous examples of the many genera of Cassiopidae found in Armenia has made a major contribution towards understanding this family. Mennessier (1984), on the other hand, although providing a world-wide compilation of all Cretaceous cassiopids, has produced an essentially phenetic and geographically-based classification. Our disinclination to adopt his latter classification has prompted this account of the cassiopid species found in the British Cretaceous. It was also decided to publish the various translations of descriptions made available to us in an attempt to assist interpretation of significant species and stabilize their nomenclature.

Records in England and earlier work

This attempt to clarify the occurrences of cassiopids in the British Cretaceous formations has necessarily been restricted to known examples in museum collections. Many of their original localities are no longer accessible. The species that do occur are restricted to the Lower Cretaceous formations of southern England.

Mantell (1833) provided the first record of a cassiopid species in Britain when he figured 'several shells ... found in ... the slabs at Pounceford' (1833: 249, fig. 3). However, that figure cannot be recognized as the *tricarinata* of J. de C. Sowerby subsequently described in Fitton (1836): see p. 259. The specimen was supposedly from the Wealden Shales at Punfield, near Swanage, Dorset, but Arkell (1941: 120) believed it to have come from the Purbeck locality of Pounceford, near Battle, Sussex (originally mentioned by Mantell) following his own comparisons with other material from there.

Table 1 The stratigraphical occurrence of species of Cassiopidae in Britain. The numbers given in brackets equal number of specimens available (see text for explanation and particularly p. 261 for clarification of records of *Paraglauconia shipbornensis*).

APTIAN (*Deshayesites forbesi* Zone; *D. callidiscus* Subzone)		
	Gymnentome pizcuetana	
[?=Crackers]	Atherfield, Isle of Wight	(5)
	[=*Gymnentome* (*C.*) *atherfieldensis*]	
	[=*Gymnentome* (*C.*) *insularis*]	
Punfield Marine Band	Punfield, Dorset	(10)
'Punfield Beds'	Punfield, Dorset	(2)
	[=*Gymnentome* (*C.*) *corfensis*]	
	Mesoglauconia renevieri	
Punfield Marine Band	Punfield, Dorset	(4)
	Mesoglauconia arkelli	
'Punfield Beds'	Corfe Castle Goods Yard	(1)
	Paraglauconia lujani	
Punfield Marine Band	Punfield, Dorset	(16)
	Worbarrow Bay, Dorset	(1)
	Corfe Castle, Dorset	(1)
? APTIAN (*D. fittoni* Subzone)		
	Paraglauconia fittoni	
? = Chale Clay	Shottermill, Surrey	(4)
BARREMIAN		
Top of Weald Clay	Haslemere, Surrey	(4)
	Huilands Farm, Surrey	(5)
Topley Bed 11	Earlswood, nr Reigate, Surrey	(8)
Lwr Cyrena Lst.	Warnham, Sussex	(1)
	Sevenoaks, Kent	(1)
Wealden Shales	Atherfield, Isle of Wight	(2)
	Corfe, Dorset	(1)
	Punfield, Dorset	(1)
? BARREMIAN, Weald Clay, Large Paludina Lst. (Topley Bed 6)		
? HAUTERIVIAN, Weald Clay, Small Paludina Lst. (Topley Bed 3)		
	Paraglauconia shipbornensis	
Weald Clay	Starve Crow, nr Tonbridge, Kent	(4)
Weald Clay	Shipbourne, nr Tonbridge, Kent	(5)
below Sdst. Bed No. 3	Clockhouse Pit, Ockley, Surrey	(9)
BERRIASIAN		
	Paraglauconia tricarinata	
[Purbeck]	[= *Paraglauconia* (*P.*) *purbeckensis*]	(1)
Corbula Bed, incl. highest Lst. band	Durlston Bay, Swanage, Dorset	(3)
Durlston Formation, Greys Lsts. Member	Pounceford, Sussex	(11)
	Burwash Wheel, nr Hastings, Sussex	(8)
	Ashdown No. 1 Borehole, Sussex	(1)

Material from Weald Clay localities in Kent and Surrey has been identified in the past as *Paraglauconia strombiformis* [=*carbonaria*], or '*Cassiope*' cf. *lujani*. Mantell (1847) was also the first to note the presence of '*Potamides*' *carbonarius* when he figured a specimen (1847: pl. 6, fig. 5) of 'this ... freshwater shell' from Compton Bay, Isle of Wight. More recently, Morter (1978: 22) concluded that the name *carbonaria* (Roemer) should only be used for the early forms and named the later Weald Clay gastropods as *fittoni*. Mennessier (1984) has described many of these specimens as distinct species (see our synonymies). Both Arkell (1941: 102) and Morter (1984) have suggested that the British provenance of some of the Mantell material (BM(NH) Mantell collection, nos. 2780–2, 12 specimens) remains in doubt owing to their uncharacteristic preservation, which is closer to that of specimens from the German Wealden.

Judd (1871: 214, 225) was the first to comment on the difficulties of cassiopid nomenclature when he described their characteristic presence in the Punfield Marine Band. He used the generic name *Vicarya*, a course also adopted by Strahan (1898). Arkell (1941, 1947) provided more precise information on their occurrence, made some palaeogeographical observations and reviewed their systematics and zoological relationships. Casey (1961) listed the Aptian species as *Cassiope*; Morter (1978, 1984) verified the occurrence of most Wealden examples and contributed to their systematic description. In this paper we recognize seven species of cassiopids within the Lower Cretaceous of Britain. After redefinition of their specific characters, in order to clarify their relationships and nomenclature, these are distributed among three described genera.

Changes in nomenclature

The following are the changes in generic or specific assignments of previously described **British taxa** mentioned in the text; changes that were made in Mennessier (1984) are marked with an asterisk.

Old assignment	New assignment
Gymnentome (*Craginia*) ***atherfieldensis*** Mennessier, 1984	= *Gymnentome pizcuetana* (Vilanova, 1859)
Eunema? ***bicarinata*** Hamlin, 1884	= *Mesoglauconia* (*Mesoglauconia*) *bicarinata* (Hamlin)*
Gymnentome (*G.*) ***corfensis*** Mennessier, 1984	= *Gymnentome pizcuetana* (Vilanova, 1859)
Cassiope ***dorsetensis*** Mennessier, 1984	= *Paraglauconia lujani* (De Verneuil & Collomb, 1853)
Paraglauconia strombiformis (Schlotheim, 1820) var. ***durlstonensis*** [=*purbeckensis*] Arkell, 1941	see under *Paraglauconia tricarinata* (J. de C. Sowerby, 1836)
Cassiope ***fittoni*** Morter, 1978	= *Paraglauconia fittoni* (Morter, 1978)
Glauconia ***frechi*** Blanckenhorn, 1890	= *Mesoglauconia frechi* (Blanckenhorn, 1890)
Cassiope ***helvetica*** (Pictet & Renevier), Arkell, 1947	= *Gymnentome pizcuetana* (Vilanova, 1859)
Gymnentome (*Craginia*) ***insularis*** Mennessier, 1984	= *Gymnentome pizcuetana* (Vilanova, 1859)
Cassiope ***lujani*** (De Verneuil & Collomb, 1853)	= *Paraglauconia lujani* (De Verneuil & Collomb, 1853)
Cassiope cf. ***lujani*** Morter, 1978 *pars*	= *Paraglauconia fittoni* (Morter, 1978)
Cassiope cf. ***lujani*** Morter, 1978 *pars*	= *Paraglauconia shipbornensis* (Mennessier, 1984)
Paraglauconia (*P.*) ***morteri*** Mennessier, 1984	= *Paraglauconia fittoni* (Morter, 1978)
Paraglauconia (*P.*) ***purbeckensis*** Mennessier, 1984	= *Paraglauconia tricarinata* (J. de C. Sowerby, 1836)
Cassiope pizcuetana var. cf. ***renevieri*** Arkell, 1947	= *Mesoglauconia* (*Mesoglauconia*) *arkelli* Mennessier, 1984*
Cassiope ***shipbornensis*** Mennessier, 1984	= *Paraglauconia shipbornensis* (Mennessier, 1984)
Paraglauconia ***strombiformis*** (Schlotheim, 1820)	= *Paraglauconia carbonaria* (Roemer, 1836)
Cassiope ***tricarinata*** (J. de C. Sowerby, 1836) Morter, 1978	= *Paraglauconia tricarinata* (J. de C. Sowerby, 1836)
Paraglauconia (*Diglauconia*) ***wassyensis*** Mennessier, 1984	= *Paraglauconia fittoni* (Morter, 1978)

Systematic descriptions

Class GASTROPODA Cuvier, 1797

? Superfamily CERITHIACEA Fleming, 1822

Family CASSIOPIDAE Kollmann, 1979
[syn. Glauconiidae Pchelintsev, 1953]

Type genus. *Cassiope* Coquand, 1865.

Diagnosis (after Akopyan, 1976: 18, 21 & 130). Conical shell, oval-conical, or conic-turreted; whorl sides generally flattened, but occasionally slightly concave in some species, or in mature

individuals of others. Ornament varies with age; composed of carinae, cords, or ridges with secondary cords, all of which may be either smooth, tuberculate, or beaded; strong carinae or keels may also develop in adult specimens. Convex base; narrow umbilicus, which may be almost concealed. Last whorl sometimes narrower, or more elongate and not conforming to the normal spiral configuration. Aperture variable from spherical to ovate; a single sinus present in the outer lip, although irregular occurrences of a second may be present, particularly in mature shells. Shell structure 'porcellaneous', cross-lamellar aragonite.

Remarks on Nomenclature. The family name Cassiopidae Kollmann (1979) replaced Glauconiidae Pchelintsev (1953: 90–91), a name based on the gastropod genus *Glauconia* Stoliczka 1868 (often incorrectly attributed to Giebel, 1852), and principally used in German-speaking countries. This name is pre-occupied by *Glauconia* Gray, 1845. Under Article 11(e) of the I.C.Z.N. (I.T.Z.N. 1985), the family name Glauconiidae is not available in the sense of Pchelintsev for the gastropods under consideration and Kollmann substituted the new name Cassiopidae.

Although the distinctive morphology of several species has been recognized for many years, there has always been considerable confusion over their determination and relationship. The nomenclature of the genera now included in the Cassiopidae has continually been misinterpreted. It is only relatively recently that Pchelintsev (1953: 91) sensibly recognized that their particular combination of shell characters warranted treatment as an independent family. After reviewing the varied opinions presented by earlier authors as to the relationships of these Cretaceous fossils, he concluded that the continual disagreement served to emphasize that such features were distinctive. Akopyan (1976) has since made a significant contribution to resolving some of the difficulties over classification of the fossil species assigned to taxa now incorporated into the Cassiopidae. Kollmann (1979) discussed the taxonomy of the family when he re-named it and also redefined several genera as well as removing others.

Characters of the Cassiopidae. One of the principal difficulties in dealing with cassiopids has been to determine what diagnostic characters might separate the relatively large number of species. Many exhibit changes in form during ontogeny, with some species being extremely variable. Cossmann (1909: 169) distinguished *Gymnentome* as a subgenus by its virtually smooth shell, only ornamented by its growth lines, and also its more pupoid and less conical shell shape. Fritzsche (1924: 38) and Steinmann (1929) also used shell shape, size and ornament to separate the species they recognized as *Paraglauconia*.

However, in common with developments in the recent classification of Turritellidae, Akopyan (1976: 20) has shown that the shape of the growth lines is of primary importance in distinguishing taxa. Using the structure of the outer lip, in particular the shape, depth and size of its outer lip sinus, together with the position of this sinus on the outer whorl, he defined seven genera. In establishing these Akopyan also used other features, namely the angle at which the growth lines met the adapical suture, and the shape of the growth lines on the lower part of the whorl. Inevitably, in defining such features in general terms there is an element of imprecision and consequently a number of species do not fit easily into his categories.

Mennessier (1984) has provided a world-wide compilation of all Cretaceous cassiopids. His use of the presence of a second basal sinus to separate two major groups is somewhat questionable, for although such a feature exists, our observations reveal that it is only markedly present at the very mature phase of shell growth, i.e. the final stages, and is then not always consistent. Such a sinus can also be seen in specimens of species belonging to genera that he has not included within his group. Consequently, we feel that such a character is too unreliable for use at this level, and for the present prefer to retain a more conservative approach when interpreting these gastropods. Hence we have only referred to his taxa in our synonymies, being disinclined to adopt the essentially phenetic and geographically-based classification he produced.

By using well-preserved specimens of most of the genera, Akopyan (1976: 19) had established that the second sinus described by many earlier workers, e.g. Zekeli (1852: 25), Reuss (1854: 886), Zittel (1882: 210), Stoliczka (1865: 12), Rehbinder (1902: 27), Cossmann (1909: 169), Douvillé (1921: 8) and Arkell (1941: 102), was never consistently present in any one specimen of

any species now included in the Cassiopidae. Therefore, it would seem that the genus *Pseudoglauconia* Douvillé [non *Pseudoglauconia* Fritzsche], which does have two distinct sinuses, should probably be placed in a different family. Kollmann (1979) omitted this genus from those he included in the Cassiopidae, but did not make any comment.

Among shell features that both Akopyan and ourselves consider to be of significance are the shape of the outer wall of the whorl, the number and formation of any keels or carinae and their resulting shoulders, or shelves, and the sequence of shell ornament development and its eventual loss. In the past, not enough use has been made of apertural shape, for the marked difference in this respect between *Gymnentome renauxiana* (d'Orbigny) and *Cassiope requieniana* (d'Orbigny) serves to establish that these species belong to quite separate genera.

PROBLEMS IN IDENTIFICATION OF SPECIES. Real difficulties occur when attributing specimens to particular species of Cassiopidae owing to the range of variation of shell sculpture and form that occurs. This is particularly true of the aperture, as indicated by growth lines. Although many authors have recognized this trait (De Verneuil & Collomb 1853; Stephenson 1952: 155; Arkell 1947: 169, Kollmann 1979 and personal communication; Kase 1984: 117) few have followed its implications when describing cassiopid species.

Ornament can vary in the following ways:

(i) the number, position and strength of both the primary and secondary spiral cords, this often resulting in different sequences;
(ii) the presence or absence, and gradual development, of nodes or tubercles on any one of these;
(iii) the shape, strength and frequency of the growth lines (which have some influence on the ornament);
(iv) the position of the sinus on the whorl;
(v) the development on the adapical part of the whorl of either a shoulder, shelf, ramp, or concavity;
(vi) the whorl profile, which may be convex, flattened, bicarinate, tricarinate, or multicarinate.

In contrast, the basal ornament generally appears to be much more consistent within a species.

In part such variation marks different stages of development within a particular species, the simpler spirals on the more pagodiform whorls representing the juvenile stages of many taxa. It is also conceivable that seasonal conditions experienced by particular individuals could influence the extent to which this condition persists. Other differences could well be the result of geographical or environmental variations, or even sexual dimorphism (e.g. see Houbrick, 1984).

Vermeij (1974), in his investigation of the differences occurring in mangrove-associated molluscs, found that such morphological diversity can be explained as a function of habitat. He noted (1974: 619–620) that the shells of species living on hard substrates had a tendency to have squat shells, whereas in those species living in soft sediments the necessity for gravitational stability was less important and diversity in form was much greater. Certain morphological peculiarities occurred in each habitat and there were consistent trends in form along habitat gradients within a number of groups. Vermeij also stated that there was abundant evidence to support the premise that the more species of a taxon which co-occur in a particular habitat, the greater will be the range of physiognomic parameters exhibited by that taxon (1974: 620); similar conclusions were reached by Houbrick (1981, 1984). It is worth noting that the variation he found in the shell morphology of western Atlantic species of *Cerithium*, e.g. *atratum*, *eburneum* and *lutosum* (Houbrick 1974), would appear to be of the same order as that found in the Cretaceous cassiopid species.

Mennessier's (1984) surmise that the cassiopids may have lived in 'mangrove-like' environments could account for the physiognomic diversity within each taxon as well as the relatively high number of species that he recognized. However, with such fossil material it is very difficult to convert shell features into suitable data for statistical analysis; furthermore, it is seldom possible to match one particular specimen precisely with another.

A number of different forms are referred to in several of the species described below, e.g. *Gymnentome pizcuetana* (p. 252) and *Paraglauconia lujani* (p. 265). In two samples of the type

species *Cassiope kefersteinii* (p. 247) from the type locality in Austria, it was possible to recognize a varying number of different forms dependent upon the weighting of their ornamental features. But measurement of these characters demonstrated that their range conformed to the frequency curve likely to occur in a single species.

The morphological distribution of cassiopids is comparable to that of their present-day ecological counterparts, where species of cerithiaceans and littorinaceans occur in separate microhabitats in the littoral environment (see pp. 280, 283). Unfortunately, with fossil taxa it is only possible to utilize criteria of geological occurrence and shell morphology to distinguish species, whereas behavioural characteristics are a major factor in recognizing species in Recent families. In closely similar species complexes, the end member of a intraspecifically variable population may be indistinguishable from a lone member of a similar species.

As noted elsewhere (p. 280), Recent intertidal Cerithiacea from comparable environments often have superficially similar species living in close proximity, often with overlapping distributions; e.g. Indo-Pacific species of *Batillaria.* Without a large series of perfectly preserved shells containing the living animals to provide the biochemical and behaviourial information necessary to establish true species, we have had to be somewhat arbitrary in determining such taxa. However, we have tried to interpret the fossil material according to our understanding of living forms. This has inevitably led us to an interpretation as to the number of species present in these Cretaceous faunas more conservative than that of most other authors.

Relationship of the Cassiopidae. The earliest member of the family recognized by us, a probably undescribed species of *Paraglauconia* (Fig. 14.10), comes from the horizon of *Indotrigonia danielli,* probably Tithonian, near Sa'ana in the SW of the Arabian Peninsula. This species has the subsutural noded spiral ribs that are found in *P. carbonaria,* together with a suprasutural carina. These ornamental features might be regarded as a primitive character.

The subsutural nodose spiral rib is shared with the more elongate Jurassic genus *Diatrypesis* Tomlin, 1929 [= *Terebrella* Andreae, 1887, *non* Maltzan, 1886]. Closely comparable species are *Diatrypesis guerrei* (Andreae) from the Oxfordian at Etivey, Yonne (see Cossmann, 1913: 149; pl. 12, figs 77, 79) and more especially *D. angustigyra* (Cossmann, 1913: pl. 12, figs 87–91) from the Upper Oxfordian at Moulins-sur-Noyers, Yonne; *Nerineopsis emarthreon* (d'Orbigny) from the Oxfordian of Neuvizi and Trouville (1913: p. 6, fig. 13; BM(NH) 70465) also shares the same ornament characters. The latter may have developed its ornament from an ancestor similar to *Rhabdocolpus* (Procerithiidae) and has traditionally been placed in the same family (Cossmann 1913). Cossmann's classification of the Cerithiacea implies a gradation from the Loxonematacea to the Cerithiacea. He suggested that the procerithiid genus *Nerineopsis* originated from the loxonematid *Protorcula* (1913: 96), which he also saw as being ancestral to the Turritellidae; whereas *Procerithium* itself was also thought to have its ancestry in the Loxonematidae, but at the Lias–Trias boundary. Procerithiids are known at a slightly earlier date than this (Haas 1953). In our view *Nerineopsis koninckii* mentioned by Cossmann (1913: 96) could just as easily be related to *Diatrypesis* and *Rhabdocolpus*, and to their common ancestor.

Many previous authors have considered that the genera now assigned to the Cassiopidae had a close relationship with the Turritellidae; e.g. d'Orbigny (1842–3), Stoliczka (1865, 1866), Rehbinder (1902) and more recently Pchelintsev (1953), Delpey (1940) and Arkell (1941, 1947). Such affinity is largely based on shell shape, ornament and some resemblance in their growth lines. Yet, we can see no evidence whatever of a filter-feeding habit in the Cassiopidae and do not think that it is at all likely for snails living in the varying salinities in which they are found. Consequently, there is no evidence that they share such a character with the Turritellidae. Neither is there any evidence of a heterostrophic protoconch occurring in the family and therefore any relationship with the Mathildidae is ruled out.

There is a strong similarity in shell ornament between some members of the Cassiopidae and the living viviparid genus *Margarya*, but we can find no earlier record of these features in the Cyclophoracea. As this living genus is restricted to certain Chinese inland waters, we can only interpret this as a case of convergence. Some species of *Bohaispira* Youlou and *Bohaispiropsis* Youlou (1978) from a Lower Tertiary brackish facies present in Bohai, north China, also have a

superficial resemblance in shell shape. There are no morphological links between the Cassiopidae and the Littorinacea, a superfamily which has spread into similar environments and whose origins are not clear.

Wenz (1939: 694) placed *Glauconia* [=*Cassiope*] within the subfamily Melanopsinae, which he included in the Thiaridae, but Morrison (1954) has explained that this was merely a convenient grouping of marginal and non-marine forms. None of the known Thiaridae, Pleuroceridae or Melanopsidae included in Morrison's classification have the distinctive shell ornament of the Cassiopidae. We are therefore of the opinion that these families are not directly related.

Other authors have suggested different affinities. Reuss (1854: 886) considered their shell characters were superficially close to *Nerinea*, only lacking the characteristic opisthobranch-like aperture and internal folds of the latter; Cossmann (1909) considered them related to the Melanopsidae of Bourguignat; while recently Morter (1978: 19) has suggested that *Cassiope* appeared to be related to the Tertiary and Recent genus *Tympanotonos* Schumacher, 1817, which belongs to the Potamididae.

As discussed above, we consider that the more primitive members of the Cassiopidae share ornament characters with the Procerithiidae, particularly the genera *Nerineopsis* and *Diatrypesis*. This evidence supports their inclusion in the Cerithiacea. It is suggested that the Cassiopidae are a distinct invasion of in-shore, brackish-water to reduced-salinity environments, and that they have evolved from the Procerithiidae. In our opinion, the Procerithiidae as at present constituted (Wenz 1939 (1961): 726–731) possibly possesses common ancestry, but gave rise to a number of different suprageneric taxa, and in a cladistic sense can be termed a 'paraphylum'.

Elsewhere, Houbrick (1981: 287) has stated that the major adaptive radiations of marine Cerithiacean families occurred at the end of the Cretaceous. Our own conjecture is that one of the initial ventures into new habitats by members of this superfamily was made much earlier by the Cassiopidae, beginning in the Jurassic and then continuing and extending during the Cretaceous.

It is not certain that the Cassiopidae survived the end of the Cretaceous; there are doubts as to whether the Eocene genus *Pseudoglauconia* Douvillé is a descendant (see p. 238); nor is there any evidence that the family gave rise to any others. Towards the end of the Cretaceous other marginally-marine cerithiaceans appear to have occupied the habitat used by the Cassiopidae.

List of genera attributed to Cassiopidae. The genera and subgenera which have been included in the family Cassiopidae by other authors (Akopyan (1976: 118), Kollmann (1979: 35), Mennessier (1984: 11) and Kase (1984: 117)) are as follows.

Araratella Akopyan, 1976. Type species: *Araratella pulchra* Akopyan, by original designation; Lower Coniacian; Azibekopv region, Gioulistan, Armenia.

Araratella (*Quadriglauconia*) Mennessier, 1984. Type species: *Turritella requieniana* d'Orbigny 1842, by original designation; Angoumian; Uchaux (Vaucluse), France.

Bicarinella Akopyan, 1976. Type species: *Pseudomesalia bicarinata* Pchelintsev 1953, by original designation; Upper Cenomanian; Armenia.

Cassiope Coquand, 1865. Type species: *Cerithium kefersteinii* Muenster *in* Goldfuss 1844, by subsequent designation by Kollmann, 1979: 36; Upper Cretaceous (? Santonian); Gosau, Austria.

Cassiope (*Cassiopella*) Kase, 1984 [non *Cassiopella* White, 1877]. Type species: *Cassiope* (*Cassiopella*) *ogai* Kase 1984, by original designation; Lower Cretaceous; Japan.

Coninoda Kollmann, 1979. Type species: *Coninoda mammata* Kollmann 1979, by original designation; Coniacian–Santonian; Hölleitengraben, Austria.

Craginia Stephenson, 1952. Type species: *Craginia turriformis* Stephenson 1952, by original designation; Cenomanian; Colorado, U.S.A.

Glauconiella Akopyan, 1976. Type species: *Omphalia undulata* Drescher 1863, by original designation; Lower Senonian; Germany.

Gymnentome Cossmann, 1909. Type species: *Turritella renauxiana* d'Orbigny 1842, by original designation; Turonian; Uchaux (Vaucluse), France.

Gymnentome (*Craginia*) Stephenson, 1952. Type species: *Craginia turriformis* Stephenson 1952, by original designation; Cenomanian; Colorado, U.S.A.

Gymnentome (*Gymnotomella*) Mennessier, 1984. Type species: *Glauconia caucasica* Pchelintsev 1927, by original designation; Upper Hauterivian; Caucasus, U.S.S.R.

Gymnentome (*Nodogymnentome*) Mennessier, 1984. Type species: *Gymnentome costata* Delpey 1941, by original designation; Albian–Cenomanian; Santorens (Aragon), Spain.

Hexaglauconia Mennessier, 1984. Type species: *Turritella coquandiana* d'Orbigny 1842 [*pars*], by original designation; Upper Santonian; Plan d'Aups (Var), France.

Hexaglauconia (*Pentaglauconia*) Mennessier, 1984. Type species: *Hexaglauconia* (*Pentaglauconia*) *tourrisensis* (Repelin 1902), by original designation; Lower Cenomanian; Tourris (Var), France.

Mesoglauconia Mennessier, 1984. Type species: *Cassiope renevieri* Coquand 1865, by original designation; Lower Aptian; Morella (Castellon), Spain.

Mesoglauconia (*Triglauconia*) Mennessier 1984. Type species: *Triglauconia margaritae* Mennessier 1984, by original designation; Albian; Bayonne, France.

Paraglauconia Steinmann, 1929. Type species: *Potamides carbonarius* Roemer 1836 [=*Muricites strombiformis* Schlotheim 1820], by subsequent designation by Mennessier, 1984; Wealden; Germany.

Paraglauconia (*Diglauconia*) Mennessier, 1984. Type species: *Cassiope picteti* Coquand 1865, by original designation; Upper Gargasian [=Aptian]–Lower Albian; Utrillas (Teruel), Spain.

The following are doubtfully included in the Cassiopidae:

Cassiopella White, 1877. Type species: *Leioplax turricula* White *in* Powell 1876, by original designation; Bitter Creek Group, ?Paleocene; Black Butte, Wyoming, U.S.A. (This was included as a subgenus of *Goniobasis* by Wenz, 1939: 699, text-fig. 2009, but it has the shell form of a cassiopid, cf. *Gymnentome* (*Craginia*)).

Pseudomesalia Douvillé, 1916. Type species: *Pseudomesalia deserti* Douvillé 1916, by original designation; Upper Albian; Gebel Manzour, Egypt.

Pseudoglauconia Douvillé, 1921. Type species: *Pseudoglauconia lissoni* Douvillé 1921, by original designation; Eocene; Negritos, Piura, Peru.

Genus *CASSIOPE* Coquand, 1865

1852 *Omphalia* Zekeli: 25–26; *non* de Haan 1825.
1852 *Glauconia* Giebel: 185; *nom. nud.*
1865 *Cassiope* Coquand: 247.
1868 *Glauconia* Stoliczka: 209; *non* Gray 1845.

TYPE SPECIES. *Cerithium kefersteinii* Muenster *in* Goldfuss 1844, by subsequent designation by Kollmann, 1978: 36.

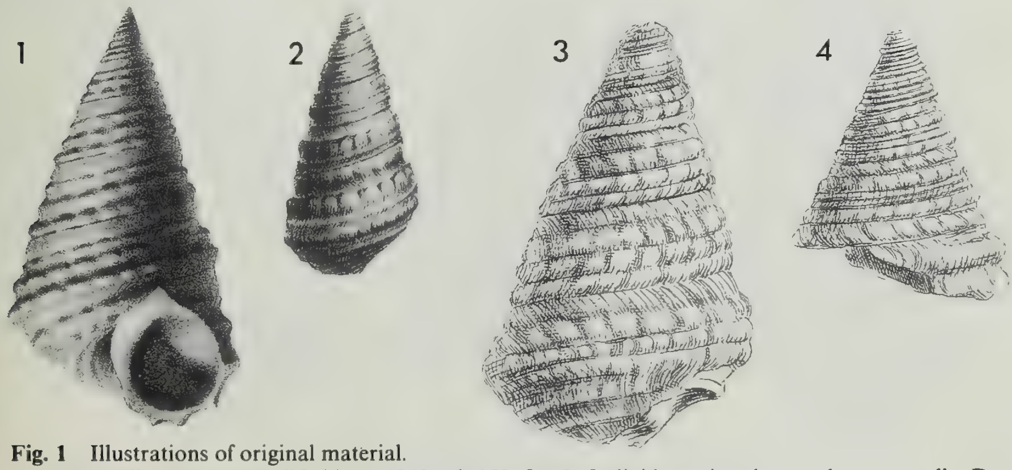

Fig. 1 Illustrations of original material.
1, *Turritella requieniana* d'Orbigny 1842: pl. 152, fig. 5. 'Individu entier, de grandeur naturelle. De ma collection'. ? From Uchaux (Vaucluse), France.
2, *Cerithium kefersteinii* Muenster *in* Goldfuss, 1844: pl. 174, fig. 11. 'In naturlicher Grosser ... bei Wienerisch Neustadt', Austria.
3, 4, *Cerithium conoideum* J. de C. Sowerby, 1832: pl. 39, figs 18 (2 figs), Gosau, Austria.

DIAGNOSIS. Broad, turriculate or cyrtoconoid shell with even whorls, which are ornamented by smooth or noded spirals. Margin of outer lip fairly deeply opisthocyrt. Basal lip weakly indented, or curved slightly in the direction of growth.

REMARKS. Cossmann (1909: 167–8) provided the first detailed description of *Cassiope*, mentioning the deep opisthocyrt growth lines and the sinus they produce in the centre of the whorl (Akopyan (1976: 20) considered the sinus was slightly above the centre). Kollmann (1979: 37) commented on earlier definitions of the genus and stated that these did not consider the great variability of form and ornament that occurred, an aspect referred to by Schenk, 1969.

Akopyan (1976: 132) described the characteristic features of *Cassiope* as 'very stocky shells with conical outlines having very strong spiral ornament of tuberculate "ribs"; these large tubercles being regularly rounded and separate from each other'. Although acknowledging the value for comparative purposes of his generalized description, we do not agree with his description of the ornament.

AVAILABILITY OF THE GENERIC NAMES. *Glauconia* Giebel (1852: 185) is a *nomen nudum* as no species are listed, no comment is made, nor is any reference given. Herrmannsen's (1852: 57) reference to the same genus is another *nomen nudum*. The first use of the name *Glauconia* in a descriptive sense for gastropods was by Stoliczka (1868: 209). Cossmann (1909: 167–8) was the first to designate *Cerithium kefersteinii* Muenster *in* Goldfuss, 1844, as the type species for this taxon, even though it was for the *nomen nudum Glauconia* Giebel; we comment upon the selection of the type species below. Thus *Glauconia* Stoliczka 1868, *non* Gray 1845, is a junior objective synonym of *Cassiope* Coquand 1865.

Cassiope Coquand (1865) is not preoccupied by *Cassiopeia* Peron & Leseuer (1810), a member of the Scyphomedusae. The different endings are real in classical language and are sufficient to avoid homonymy; see I.C.Z.N., Article 57 (f) (I.T.Z.N. 1985: 109).

Coquand (1865: 247) introduced the name *Cassiope* explicitly as a replacement name for *Omphalia* Zekeli 1852 (*non Omphalia* de Haan 1825, type species *Nautilus umbilicatus* Linné, by

Fig. 2 *Cassiope suffarcinata* (Muenster *in* Goldfuss, 1844). 1, 2, EM 30423; 3, EM 30422; all ×2. De Verneuil colln, 1873, from Gosau, Austria; École des Mines colln, Paris but at present in Lyon. Figd by Mennessier (1984: pl. 9, figs 11a, b, 12) as '*Hexaglauconia suffarcinata* (Muenster, ? 1844/47)', together with BMNH specimen G.17915 (see Fig. 3.2, 3).

original designation; a use which has often been overlooked and is a junior subjective synonym of *Nautilus* Linné), as follows:

Notre genre *Cassiope* comprend le genre *Omphalia* de Zekeli, qui, lui-même, était un démembrement du genre *Turritella*. Le nom d'*Omphalia* ne pouvait être conservé, car il avait été déjà appliqué en 1825 par M. de Haan à un groupe de Nautiles. M. Pictet fait observer en outre qu'il existe un genre *Omphalius*, Philippi, établi en 1847 sur le *Trochus rusticus*, etc.

THE TYPE SPECIES OF *Cassiope* COQUAND. When a new name is proposed expressly as a replacement for a prior name, as in the case of *Cassiope*, the type fixation must be the same for both (Article 67 (h); I.T.Z.N. 1985: 125), and only names explicitly mentioned by an author in his original list either as valid names, or as synonyms, are available for selection as type species of a genus (Article 69 (a) (i); 1985: 133).

The original list of nine species included in *Omphalia* by Zekeli (1852: 119) contained twelve binomina, three of which were considered to be junior synonyms of the first:

Omphalia conica Zekeli 1852
Cerithium conoideum J. de C. Sowerby 1832, *non* Lamarck 1804
Cerithium conica Muenster *in* Goldfuss 1844
Turritella requieniana d'Orbigny 1842
Omphalia coquandiana (d'Orbigny 1842)
Omphalia kefersteini [sic] (Muenster *in* Goldfuss 1844)
Omphalia ovata Zekeli 1852
Omphalia suffarcinata (Muenster *in* Goldfuss 1844)
Omphalia giebeli Zekeli 1852
Omphalia turgida Zekeli 1852
Omphalia subgradata Zekeli 1852
Omphalia ventricosa Zekeli 1852

Despite the number of species described by the earlier authors, we feel that there was some attempt at that time to resolve the nomenclatorial problems. It was realised in Goldfuss (1844) that the earliest name of *conoideum*, given by J. de C. Sowerby, had to be replaced, and *conicum* was used instead for that species. D'Orbigny (1842: 43) had, however, also recognized the need slightly earlier; he had identified it as *Turritella requieniana*, but this is now distinguished as a separate species.

The first group of names on the above list were considered to be synonyms by Zekeli, who used the name *Omphalia conica* Zekeli. This might be construed as a validation of that specific name. However, there are older names available for this species which, following the nomenclatorial actions mentioned below, should be known as *Cassiope kefersteinii* (Muenster *in* Goldfuss). The earliest valid name available for Sowerby's species appears to be *suffarcinata* Muenster *in* Goldfuss, 1844.

Kollmann (1979: 36) followed Cossmann and designated *Cerithium kefersteinii* Muenster *in* Goldfuss, 1844, as the type species when he redefined the genus as *Cassiope*, and Kase (1984) has followed this. Akopyan (1976: 131) quoted *Cerithium kefersteini* [sic] Goldfuss as the type species of *Glauconia*, his understanding of which resembles our present interpretation of *Cassiope*.

Morter's (1978: 21) selection of *Cerithium lujani* de Verneuil 1853 as type species of *Cassiope* is invalid, as neither that species, nor any synonym of it, was on Zekeli's original list of species; similarly, the use by Mennessier (1984: 77) is also incorrect.

Cassiope kefersteinii (Muenster *in* Goldfuss, 1844)
Figs 4–6

1844 *Cerithium kefersteinii* Muenster *in* Goldfuss: 36; pl. 174, fig. 11.
?1852 *Omphalia kefersteini* Zekeli: 27; pl. 2, figs 3c, d (*non* figs 3a, b, = *C. bicostata* (Schenk)).
?1909 *Glauconia kefersteinii* (Goldfuss) Cossmann: 167; pl. 4, fig. 3.
non 1939 *Glauconia* (*Glauconia*) *kefersteini* (Goldfuss); Wenz: 694–695, fig. 1997 [? = *C. bicostata* (Schenk)].

non 1964 *Glauconia* (*Glauconia*) *coquandiana kefersteini* (Münster); Benkö-Czabalay: 164–165; pl. 2, figs 1–8 [? = *kuehni* Benkö-Czabalay].
?1969 *Glauconia* (*Glauconia*) *kefersteini kefersteini* (Muenster); Schenk: 52; pl. 1, fig. 23; pl. 2, fig. 1.
?1969 *Glauconia* (*Glauconia*) *ornata* (Drescher); Schenk: 68; pl. 2, figs 4a–c.
1979 *Cassiope kefersteini* (Goldfuss) Kollmann: 36–37.
1984 *Araratella* (*Quadriglauconia*) *kefersteini* (Goldfuss) Mennessier: 36; pl. 10, figs 6–10.
1984 *Hexaglauconia* (*Hexaglauconia*) *schenki* Mennessier: 46; pl. 10, fig. 10, ? fig. 9.
?1984 *Hexaglauconia* (*Hexaglauconia*) *fallaciosa* Mennessier: 43; pl. 11, figs 2–3.

Diagnosis. A very variable cassiopid ranging from slender, essentially pagodiform, simple spirally-ornamented forms, to broader, bicarinate or slightly tuberculate shouldered shells. The sinus of the opisthocyrt growth lines occurs in the upper third of the whorl and is itself influenced by, and in turn affects, the shell ornament. The base is characteristically ornamented by three strong, raised, essentially smooth spiral cords.

Original descriptions. Muenster (1844: 36) [translation]: 'Conical top-shaped, with 10 almost quadrangular whorls, that are stepped-off above their middle and pressed tight against each other; they have undulating ribs throughout their length and in their thicker lower halves are surrounded by three girdles. The uppermost of these lies on the angle and is provided with

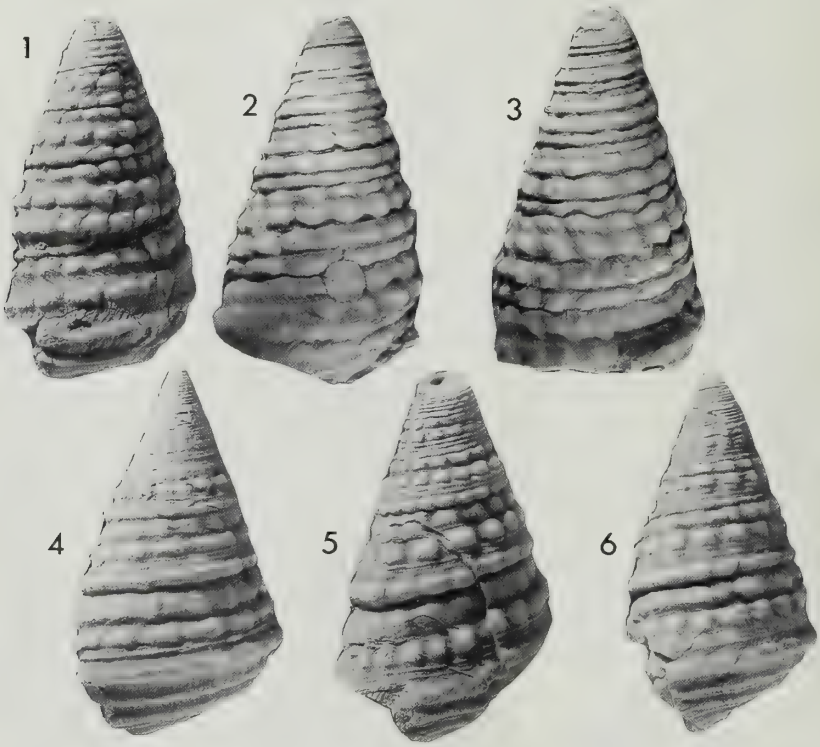

Fig. 3 *Cassiope suffarcinata* (Muenster *in* Goldfuss, 1844). **1**, *Cassiope* ? *lanzingensis* (Mennessier). BMNH GG.14391, ×1; colld N. J. Morris; Coniacian, Gosau Beds, Lanzing, nr Miesenbach, Austria. **2, 3,** different views of the lectotype of *Cerithium conoideum* J. de C. Sowerby 1832, *non* Lamarck 1804. BMNH GG.20927 (*ex* G.17915), Gosau, Austria, ×1·5. Murchison colln, transferred from the Museum of Practical Geology in 1880. Figd by J. de C. Sowerby (*in* Sedgwick & Murchison 1832: pl. 39, fig. 18 left); also figd as *Araratella* (*Quadriglauconia*) *conoidea* (J. de C. Sowerby) by Mennessier (1984: pl. 6, fig. 19). See also Fig. 6.7. **4, 5, 6,** specimens showing variation in ornament; all from 'Gosauschichten', Gams, 'Steyermark', Austria; purchd from Dr A. Krantz; all ×1; 4, BMNH 66257; 5, GG.14394; 6, GG.14395.

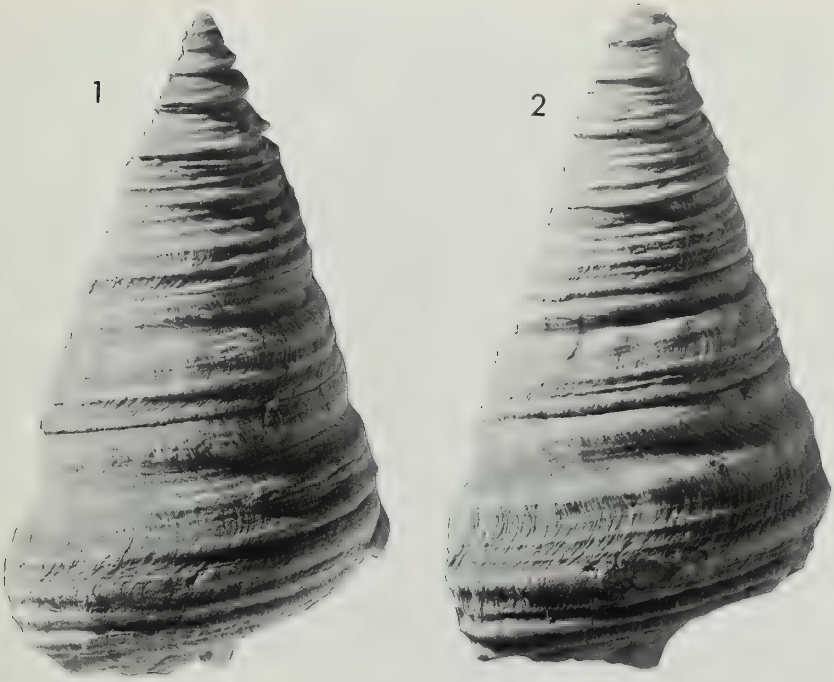

Fig. 4 *Cassiope kefersteinii* (Muenster *in* Goldfuss, 1844). 1, no. 1985/65 16F; 2, **neotype** (herein designated), no. 1985/65/1; both Fürst colln from Gosauschichten, Dreistetten no. 5, Austria; × 3·5. Geologisch-paläontologische Abteilung, Naturhistorisches Museum, Vienna.

thick flat tubercles on the last and penultimate whorl, but in the other whorls is smooth and split into two lines. The two lower girdles are smooth and only half as wide. The narrower part of the last whorl reveals half-erased tubercles; on the penultimate whorls, however, these are smooth.'

Zekeli (1852: 27) [translation]:'

Conical top-shaped with a narrow umbilicus with whorls of various shapes that are differently and densely ribbed; these whorls are partly tetragonal and in contact with each other, but above their middle part are stepped off, and on the thicker lower halves are surrounded by three girdles and show the development of nodes by means of the regularly-spaced brown-coloured growth lines; other whorls are slightly convex separated by a sutural furrow and set off in the centre while below they are expanded convexly; they are smooth throughout and either carry four strong transverse lines of variable fineness, or very numerous very fine transverse lines. Others overlap each other like a staircase and are surrounded with many smooth spirals which are set off against the suture beneath a strong angle.

Mennessier (1984: 36): 'Small size, rather slender; imbricate; three principal cordons, rather narrow and slightly nodulose; concave shoulder/ramp carries a very weak cord.'

Original material. Muenster considered that *C. kefersteinii* was distinct from *conicum*, the replacement name he had provided for *conoideum* J. de C. Sowerby, *non* Lamarck [=*pseudoconoideum* d'Orbigny, see p. 247]. The original specimen of *kefersteinii* was once in the Museo Borussicae (and probably in the Bonn Museum), but we have been unable to examine it, because it cannot be found (Dr H. Remy, personal communication 1984, and see also Mennessier, 1984: 36). We have also enquired for the original material at those institutions known to have some Goldfuss material (Dr H. Jaeger at the Humboldt Museum, and Dr G. Schairer in the Bayerische Staatssammlung, Munich), but without success. We have therefore concluded that there are no extant type specimens of *Cerithium kefersteinii*. Neither has it been possible to examine the specimens figured under this name by Zekeli or Cossmann.

Fig. 5 *Cassiope kefersteinii* (Muenster *in* Goldfuss, 1844). Variation in ornament occurring within this species; note the varying position and strength of the spiral cords. All specimens from the Gosauschichten, Dreistetten, Neue Welt, Austria. Left to right: 14F; 6C; 19F (=neotype, see Fig. 4.2); 37C; 13C; 16C. All specimens in Geologisch-paläontologische Abteilung; Naturhistorisches Museum, Vienna; numbered 1985/65/6, 2, 1, 5, 3 and 4 respectively; all ×3·5.

Zekeli's (1852: pl. 2, figs 3a–e) material is at present in the collections of the Geological Survey of Austria. Most of these, however, do not appear to conform with earlier, or subsequent, interpretations of the species. Mennessier (1984) has placed some of these fossils in two different species of his new genus *Hexaglauconia* and discounted others as even being cassiopids. Wenz' (1939: 694, fig. 1997) figure is merely a copy after Zekeli (1852: pl. 4, fig. 3a).

Cossmann's (1909: 168; pl. 4, fig. 3) specimen is thought to be in the Université de Paris VI, but these collections are not readily accessible (*fide* Dr P. Bouchet, personal communication). It has been assigned by Mennessier (1984: 41) to his new species *Hexaglauconia* (*H.*) *austriaca*, but we feel that it could come within the range of variation shown by specimens of *kefersteinii*.

Neotype (herein designated). No. 1985/65/1, Fürst Collection; Gosau-Schichten; Dreistetten No. 5, Austria. Geologisch-paläontologische Abteilung, Naturhistorisches Museum, Vienna. We have chosen a specimen that most closely resembles the original figure published in Goldfuss. This was done after an unsuccessful attempt to locate the original figured specimen (see above), as we believe it is necessary to establish the identity of the type species of the genus *Cassiope*.

Other material studied. In Vienna, Geologisch-paläontologische Abteilung, Naturhistorisches Museum, the following in addition to the Neotype: Gosau-Schichten; Dreistetten No. 15, Chlupac Collection (38 specimens: 1–38C; nos 6C, 13C, 16C, 37C = 1985/65/2–5 respectively). Gosau-Schichten; Dreistetten No. 5, Fürst Collection (21 specimens: 1–19F; nos 14F and 19F = 1985/65/6 and 1985/65/1).

In London, Department of Palaeontology, BM(NH): G.92620–1, from Brandenberg, Tirol, pres'd Dr Ogilvie-Gordon, 1938; G.28221–5, Traunwand, Gosau, A. Schrammen Coll'n, purch'd 1920 (includes 4 juveniles). GG.14406–9 (12 specimens), from Schneckengartl, nr Dreistätten; GG.14393 (2 specimens), from Lanzing, Miesenbach; GG.14393, from Gams, Styria; all collected by N. J. Morris, July 1985.

DISCUSSION. Muenster (1844) recognized the characteristic ornament and variation of *C. kefersteinii*. Zekeli (1852), on the other hand, confused the interpretation of this species by including other cassiopids within the range of ornament he described. *C. kefersteinii* is perhaps most easily distinguished from contemporaneous species by its less frequent development of tubercles, or nodes, on the spiral cords. In general, the spirals are simple and quite frequently narrow, or even fine; it is only in the more extreme forms such as the Neotype that tubercles are developed on the adapical spiral cord, or on the cord occurring at the ramp angle. The early whorls of *kefersteinii* are essentially pagodiform, ornamented by a number of simple, evenly spaced, spiral cords, which become stronger and more prominent at the abapical suture.

Schenk (1969: 52) provided a more detailed description of this species and recorded the differences in shell morphology and ornament of forms from various Austrian localities. His readiness to accept the considerable variation in shell form exhibited by these specimens attributed to *kefersteinii* has not been followed by Mennessier. The latter (1984) has listed some fourteen nominal species from Austrian Cretaceous material and interpreted *kerfersteinii* solely as the Brandenberg form figured by Schenk.

Dr Heinz Kollmann has kindly provided us with information on the occurrence of this species and a series of specimens. It is generally realised that the locality given in the original description is inaccurate, for Wiener Neustadt lies within the Vienna Tertiary Basin. However, there are a number of Cretaceous exposures several kilometres to the west of that town (e.g. Grünbach, Neue Welt, Lanzing etc.). Kollmann remarked (personal communication) that 'none of them can be excluded but ... it seems most likely that Schneckengarten, close to the village of Dreistätten, is the type locality'. In answer to our queries concerning the possibility of the various forms being restricted to particular horizons in the Cretaceous sequence, he believed this was extremely unlikely. He also considered that the different types of sediment apparently associated with some of the specimens were probably the result of variations in weathering.

Twelve or more different combinations of ornament development and shell shape can be distinguished within the sample provided from the type locality. However, when plotted on a simple block diagram, these conform to the normal range shown by a single species. Furthermore, plotting the measurement of height against width, and also those of the sinus on the last whorl, produces patterns consistent with their belonging to the same species.

Schenk (1969: 58) described a cassiopid in which the whorls are ornamented by two very strong bicarinate spiral cords as *kefersteini bicostata*, but Mennessier (1984: 46) considered it to be a separate species of *Hexaglauconia*. However, we prefer to recognize this as another species of *Cassiope*, possessing the typical pagodiform juvenile ornament.

The abundance of cassiopids in the Upper Cretaceous Gosau Formation of the eastern Alps has led to a profusion of names. Unfortunately, despite recent studies (Kollmann 1979, Schenk 1971, Mennessier 1984) their nomenclature has not been resolved and we do not believe that several of the species described are sufficiently distinct. The position and sequence of primary and secondary spiral cords, together with the degree and number of their noded/tuberculate ornament, varies considerably in all these Austrian cassiopids. Inevitably, although the sinus in the growth lines occurs in virtually the same position on the whorl, it coincides with different elements of the ornament, in some being between the cords and in others situated on one of them.

We suspect that different forms of the same species predominate in particular in-shore habitats preserved in the Austrian Upper Cretaceous. However, it is necessary to make more detailed studies of the occurrence of these cassiopids and their variation in ornament before the history of the family can be adequately understood. For the moment we can only recognize *kefersteinii*, *bicostata* and *suffarcinata* [= *pseudoconoideum* d'Orbigny, which is available for the

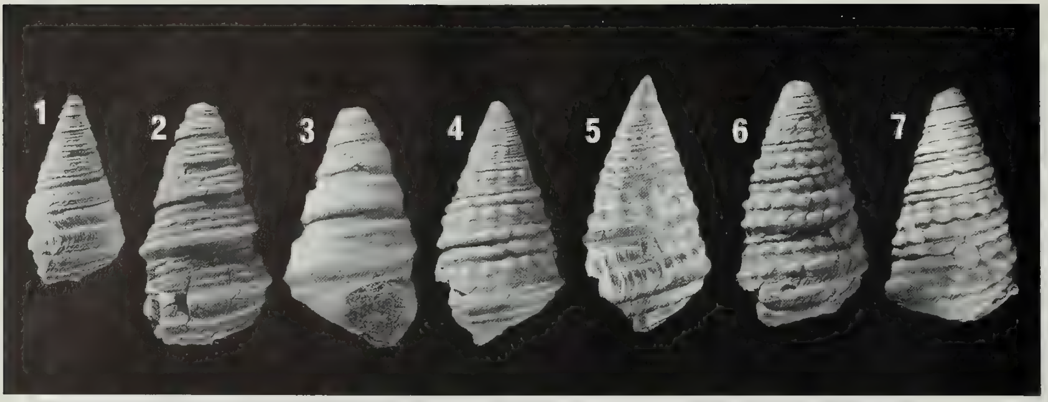

Fig. 6 Austrian cassiopids.

1, *Cassiope kefersteinii* (Muenster *in* Goldfuss, 1844). Gosauschichten, Upper Coniacian; Dreistetten no. 5; Fürst colln (19F), Naturhistorisches Museum, Vienna; ×0·9.

2, 3, specimens from Bed f, Zottbach, Brandenberg, Austria; colld N. J. Morris, June 1985. 2, *Cassiope ? kefersteinii* var.; BMNH GG.14380, ×1·1. 3, *Cassiope bicostata* (Mennessier); BMNH GG.14382, ×1·0.

4, 5, *Cassiope suffarcinata* (Muenster *in* Goldfuss, 1844). 4, ? cf. *coquandiana* (Zekeli); BMNH GG.14395, ×0·95; Gams, Steiermark; purchd from Dr A. Krantz. 5, EM 30423, ×0·5; 'Gosau'; formerly in École des Mines, Paris and now in Dept des Sciences de la Terre, Lyon; De Verneuil colln.

6, *Cassiope lanzingensis* (Mennessier, 1984). BMNH GG.14391, ×0·7; Lanzing, Miesenbach; colld N. J. Morris, June 1985.

7, *Cassiope suffarcinata* (Muenster *in* Goldfuss, 1844). BMNH GG.20927 (*ex* G.17915), ×0·9; lectotype of *Araratella* (*Quadriglauconia*) *conoidea* (J. de C. Sowerby, 1832, *non* Lamarck 1824) Mennessier, 1984; 'Gosau'; Murchison colln. See also Fig. 3.2, 3.

invalid *conoideum* J. de C. Sowerby] as species of *Cassiope*, and believe that several other described species are merely synonyms of these. (A Neotype of *C. suffarcinata* was selected by Mennessier (1984: 42, 141; pl. 9, figs 9a–c) from the material in the collections of the Geological Survey of Austria, Vienna.) We are uncertain whether the form shown here (Figs 3.1 and 6.6), obtained from underneath the coral–rudist bed at Lanzing and described as *Hexaglauconia* (*H.*) *lanzingensis* Mennessier, is distinct from *C. suffarcinata*. It is ornamented by evenly-distributed noded spiral cords, in contrast to the more closely-packed cords present on the type of *suffarcinata* [=*conoideum*], but is very similar to the forms of the latter shown in Fig. 3.

Lack of sufficient material prevents us from considering the species *giebeli* and *gamsensis* (which Mennessier (1984) placed in the genus *Gymnentome*), and for the present we accept their assignments.

Genus *GYMNENTOME* Cossmann, 1909

Type species. *Turritella renauxiana* d'Orbigny 1843, by original designation. Mennessier incorrectly designated as lectotype a specimen of *G. renauxiana* in the Dumas Collection in the Nîmes Museum; it was from the type locality of Uchaux and had been figured by Mazeran (1911).

Discussion. Cossmann erected *Gymnentome* as a section of the genus *Glauconia*. His diagnosis is widely accepted for those members of the family having a smooth, convex shell, only ornamented by growth-lines having a relatively narrow, deep V-shaped sinus about the centre of the whorl. However, Akopyan (1976: 20) considered the sinus to be slightly below the centre. Kollmann (1979: 37), when assessing the features of *Gymnentome*, provided details of its evolutionary reduction of ornament and gave a more precise description of its growth-line shape. We have not attempted to use the divisions of *Gymentome* s.str. adopted by Mennessier.

According to d'Orbigny, the type species occurs at four localities in southern France: Uchaux (type locality) and Mondragon (Vauclause); La Cadière and Sainte-Baume (Var): exposures at these localities range from Turonian to lower Campanian in age. However, later authors have recognized some of these specimens as belonging to other species, e.g. *gibbosa* (Repelin) and *caderensis* (Repelin); see Mennessier (1984: 68–71).

The genus ranges from the Albian to the Cenomanian and the inclusion of *G. pizcuetana* (Vilanova) would extend this back into the Aptian. If one followed Mennessier (1984: 66–74) the range would be Berriasian to Campanian, but we doubt whether all the species he lists should be included; relevant literature also indicates that the ages of several are wrongly ascribed. Yet, the very small shells from the Upper Valanginian–Barremian found in the Province of Rioja, Spain, and described as *Paraglauconia* (*Diglauconia*) *vierai* by Mennessier & Calzada (1985: 139, 142; figs 1, 3, 4), would appear to have some affinity with *Gymnentome* and indicate its earlier occurrence. These relatively smooth cassiopids have growth lines and shells that are closely comparable to those of other later species of *Gymnentome*; they would seem to be misplaced in *P.* (*Diglauconia*) as their ornament does not conform to the diagnosis of that subgenus! It is possible that *G. pizcuetana* represents the stock from which many European species have evolved and this could account for its dissimilarity from the commoner, less ornamented, later forms that are readily recognized as *Gymnentome*.

Gymnentome pizcuetana (Vilanova, 1859)
Figs. 7, 8

1859 *Pleurotomaria pizcuetana* Vilanova: pl. 2, fig. 12.
1865 *Cassiope pizcuetana* (Vilanova) Coquand: 248; pl. 3, figs 1, 2.
1865 *? Cassiope zekellii* Coquand: 248–9; pl. 3, fig. 3.

Fig. 7 *Gymnentome pizcuetana* (Vilanova, 1859). **1**, BMNH G.7810, H. S. Beckles colln; Crackers, Atherfield, Isle of Wight. An elongate form, figd by Arkell (1947: fig. 37.2) and the holotype of *Gymnentome* (*Craginia*) *atherfieldensis* Mennessier (1984: pl. 19, fig. 3); ×1 approx. **2**, IGS 70316, 'Punfield Beds', Goods Yard, Corfe Castle. Holotype of *Gymnentome corfensis* Mennessier (1984: pl. 25, fig. 9); ×1. **3**, IGS 56817, E. Forbes colln, Punfield, Dorset, horizon not known; ×0·75. **4**, BMNH GG.21420, Martin Simpson colln, Punfield Marine Band, Punfield Cove, nr Swanage, Dorset; ×1·25. **5**, BMNH GG.21551, I. Gurrea colln, presd 1984. Lower Aptian, Castellón, Spain; ×0·75 approx.

1868 *Vicarya pizcuetana* (Vilanova) De Verneuil & Lorière: 4–5; pl. 1, fig. 2.
1940 *Glauconia* (*Glauconia–Gymnentome*) *pizcueti* (Vilanova) Delpey: 105, fig. 75 [incorrect emend.].
1947 *Cassiope pizcuetana* (Vilanova); Arkell: 168, fig. 37.2.
1947 *Cassiope helvetica* (Pictet & Renevier); Arkell: 168, fig. 37.8.
1984 *Gymnentome* (*Craginia*) *pizcuetai* (Vilanova) Mennessier: 61–2; pl. 18, figs 8–10 [incorrect emend.].
1984 *Gymnentome* (*Craginia*) *pizcuetai* var. *carinata* Mennessier: 62; pl. 18, figs 11–12.
1984 *Gymnentome* (*Craginia*) *atherfieldensis* Mennessier: 63; pl. 19, figs 3–4.
1984 *Gymnentome* (*Craginia*) *insulcris* Mennessier: 62; pl. 18, fig. 14.
1984 *Gymnentome* (*Gymnentome*) *corfensis* Mennessier: 74; pl. 25, figs 9, 10.
1984 *? Gymnentome* (*Craginia*) *zekelii* (Coquand) Mennessier: 62; pl. 18, fig. 13.
1984 *? Gymnentome pizcuetana* (Vilanova); Cleevely *et al.*: 96, 98; figs 2.13, 2.14.

DIAGNOSIS. Large, variable, thick-shelled cassiopid with smooth convex whorls, ornamented by strong mid-whorl rounded carinae, with a distinctive shelf or shoulder occurring above the more dominant uppermost carina; the opisthocyrt growth lines have a wide, shallow sinus situated at the centre of the whorl.

Mennessier (1984) diagnosed the species as of very large size; massive form; anterior cordon predominates on later whorls and forms a ramp; easily distinguished from other species by its great size and the richness of its ornament.

TYPE MATERIAL. Vilanova's specimens are thought to be in Madrid, either at the Museo Nacional de Historia Natural, or in the Instituto Geologico y Minero de España, but attempts to confirm their existence in either of these collections have not met with any success. It is believed that the type material has been mixed together with other fossils (S. Calzada, personal communication, 1984). Mennessier (1984: 62) erected a neotype after stating that the holotype was lost and selected a specimen available to him from a different locality. This would seem to be unnecessary, for it should be possible to recognize the holotype, if is amongst the material that has survived.

Fig. 8 *Gymnentome pizcuetana* (Vilanova, 1859). **1**, BMNH GG.21421, M. Simpson colln, Punfield Marine Band, Punfield Cove, Dorset; strongly rounded carinate form cf. *turgida* (Zekeli); ×0·75. **2**, BMNH 46455, purchd from B. Wright, ?Crackers, Isle of Wight. An angular variety of *pizcuetana*, described as the holotype of *Gymnentome* (*Craginia*) *insularis* Mennessier (1984: pl. 18, figs 14a, b); ×0·75. **3**, BMNH 46031, purchd from M. J. Rothschild, 1864, its locality recorded as Morella, Spain; ×1 approx.

British material. Punfield; Punfield Marine Band: BM(NH) G.8834 (3 specimens); G.20882, Caleb Evans coll'n; GG.9333–7 (=5 specimens); GG.21413–4; GG.21416–8; GG.21420–3, M. Simpson coll'n; GG.21429. IGS 56817, E. Forbes coll'n.

Punfield Beds: IGS 35711, Punfield, Swanage Bay, Dorset. IGS 70316, Geol. Survey coll'n, 1889; Goods Yard, Corfe Castle, Dorset; the holotype of *Gymnentome* (*G.*) *corfensis* Mennessier (1984: pl. 25, fig. 9).

From Atherfield, Isle of Wight, (horizon not certain, ? Crackers): BM(NH): G.7810 (2 specimens), holotype and paratype of *Gymnentome* (*Craginia*) *atherfieldensis* Mennessier (1984: pl. 19, figs 3, 4). 46455, ? holotype by monotypy of *Gymnentome* (*Craginia*) *insularis* Mennessier (1984: pl. 18, figs 14a, b); all H. S. Beckles coll'n. 48626 (2 specimens), Saxby coll'n.

Material from Spain. In BM(NH): 46031, from Morella, purch'd from M. J. Rothschild December 1864; GG.21551, Lower Aptian; Castellón, I. Gurrea coll'n, pres'd 1984.

In École des Mines, Paris (specimens at present in Dépt. des Sciences de la Terre, Lyon): EM 30417, De Verneuil coll'n, San Mateo; EM 30418–9, Deshayes coll'n, Chert (it is possible that this material could have been obtained from Vilanova); EM 30420, Teruel.

In Magyar Állami Földtani Intêzet., Budapest; ? H. Coquand coll'n: K 3180 (1) from Gargallo; K 3184 (2) from Arcaine; K 3175 (5) from Obon; K 9636 (1) from Obon (labelled as *heeri*). Our interpretation of these Budapest specimens from photographs suggests that several may belong to other taxa, e.g. *P. lujani* or *M. renevieri*, rather than to *pizcuetana*, for they are quite strongly ornamented and appear to have a sharper sinus in their growth lines.

Coquand (1865) recorded this species from fourteen different Cretaceous localities in Spain; De Verneuil & Lorière (1868: 5) listed a number of these including the probable type locality Chert (Castellón); Mennessier quoted 31 localities from Bataller (1949). It would appear that *pizcuetana* is widespread throughout the Lower Aptian, occurring at localities from Lebanon in the east to Spain in the west and extending north as far as the U.K.; at each of these occurrences it is associated with marine faunas.

Description. Our translation of Coquand's original description is as follows:

Shell thick, with conical spire, umbilicate, composed of rounded whorls from seven to eight in number, ornamented by three spiral cords, smooth, that which towers over the apical suture is the most considerable and dominates the two others, seen on the last two whorls. The suture is a little more pronounced than the furrow which separates the two cords. The last whorl shows, beneath the dominant cord, three other very fine cords equidistant from each other. Aperture entire, enlarged, narrow, compressed by large median fold, which gradually becomes smaller and completely disappears towards the last third of the whorl, which is narrower than the previous ones. The shell, especially in the buccal region, shows feeble growth lines, which are inflexed backwards in their centre. (Coquand, 1865).

The early whorls are ornamented by simple spiral cords, two of which form equally strong carinae near the middle of the whorl. The uppermost mid-whorl carina gradually becomes the more dominant, although a transitional stage of relatively smooth whorls with a slightly noded cord, or else a series of flattened spirals, may intervene. The typical adapical shelf is present from the fifth or sixth whorl. Many specimens show the narrowing and elongation of the final whorl mentioned by Coquand. In addition to the primary cords and carina, several fine secondary spirals may occur on all later whorls.

Discussion. Coquand's description contains the essential characters of this species and these have been augmented by later authors. De Verneuil & Lorière (1868) emphasized its great variability and recognized two main forms (see their figs 2b, c) but with many intermediates between them. Mennessier (1984: 62), who took a much narrower view of the range shown by *pizcuetana*, has surprisingly placed both these extreme members in his var. *carinata*, but we suspect that he only intended to list the specimen shown in fig. 2c.

Coquand, after he had prepared a figure and named a specimen in recognition of his contemporary, realised that *Cassiope zekellii* was a very elongate form of *pizcuetana*. But with so few specimens available we are uncertain whether this really is an extreme form of *pizcuetana*, or a separate species that would be more correctly placed in *Craginia* Stephenson. Mennessier

adopted that course, but reduced this hitherto solely North American genus to a subgenus of *Gymnentome*. We are extremely doubtful whether the majority of the non-American species are correctly assigned. The British Lower Cretaceous specimens do not belong to *Craginia* for they do not have large turreted shells, nor do they possess comparable growth lines.

Zekeli's figure (1852: pl. 3, fig. 2) shows that *Omphalia turgida* Zekeli from Windischgarten (Austria) is very similar to *pizcuetana*, especially BM(NH) specimens G.20882 and GG.21421 from the Punfield Marine Band and 46455 from the ? Crackers. Yet the Gosauschichten from which *turgida* was described is of Coniacian–Santonian age. Both Akopyan (1976) and Mennessier (1984) have included *turgida* in *Gymnentome*, but the latter has questioned its provenance.

Another Upper Cretaceous species from the same Austrian formation, *'Omphalia' giebeli* Zekeli (1852), would appear to be more reminiscent of ? *G. pizcuetana* in size, shape, growth lines and sequence of ornament. Our comparison is based upon the original figure (1852: pl. 3, fig. 1a) and three specimens: BM(NH) 52118 and 66256 from Gams in Steiermark, and another, G.17834, merely marked Gosau, Austria. All possess growth lines having the wider sinus characteristic of *pizcuetana* rather than the much narrower V-shaped sinus given as typical of *Gymnentome* s.str. (see Akopyan, 1976: 20). They differ in not having any strong spiral cords, particularly the more obvious carinae of *pizcuetana*'s later whorls, and in this respect are similar to the much smoother *G. renauxiana* (d'Orbigny). Mennessier (1984: 151) appears to have selected a rather different shell as lectotype of *giebeli* (Zekeli), whilst the specimens we

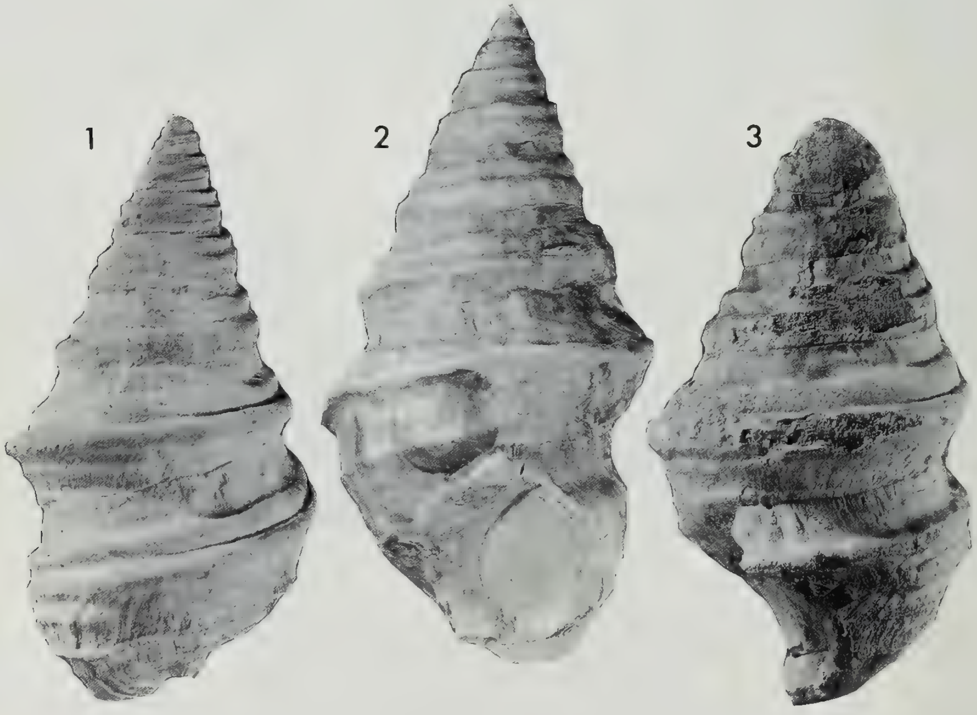

Fig. 9 Examples of the more irregularly and coarsely ornamented forms of *?Gymnentome pizcuetana* (Vilanova, 1859) from localities in Spain; all the specimens belong to the École des Mines collection, Paris, but at present in Lyon. **1**, EM 30417, De Verneuil colln, 1873, from San Mateo; cf. Vilanova (1859: pl. 2, fig. 12); × 1. **2**, EM 30418, Deshayes colln, 1867, from Chert, Castellón; × 1. **3**, EM 30420, an iron-stained specimen from Utrillas, Teruel, cf. De Verneuil & Lorière (1868: pl. 1, fig. 2c); × 1.

have accepted as *giebeli* (including material examined in the De Verneuil collection now at Lyons) he has named *gamsemsis* (1984: 71).

Mennessier recognized that his *G.* (*Craginia*) *nipponica* (1984: 63) from the Upper Albian–Turonian of Japan was very close to *pizcuetana.* We also feel that the specimens originally assigned to *pizcuetana* from the Aptian of Temska, Serbia, Jugoslavia, which he has since described as *G.* (*Craginia*) *temskensis*, could well be conspecific. In fact, together with others of his *G. renauxi* group, especially *G. transylvanica* Mennessier, these should be placed with *pizcuetana.*

Delpey (1940) was somewhat uncertain over assigning *pizcuetana* to *Gymnentome* and preferred to suggest that it was possibly intermediate between *'Glauconia'* and *Gymnentome* and perhaps the ancestor of the latter, a view first postulated by Repelin (1902). Our own attribution of this species to *Gymnentome* is also made with considerable reservation. We recognize that its growth lines, in particular the shape and position of the sinus, together with its distinctive and variable sequence of shell ornament, do not conform with the essential characters of that genus. However, it is equally if not more distinct from *Cassiope* s.str., and also from the various new genera raised by Mennessier. Consequently, we cannot disagree with Delpey's postulation as to the probable phylogenetic position of *pizcuetana.*

The British material is slightly different from the form commonly found in Spain (Mennessier has described them as distinct species), although examples of the Iberian form also occur amongst those in the Punfield Marine Band. It is difficult to offer a satisfactory explanation for these differences as the total number of specimens available to us is far too small for any serious assessment. The larger size and grosser ornament of the Spanish material might be regarded as a gerontic condition, or alternatively might be the result of ecological differences, but we tend to believe that the majority represent different growth stages.

Amongst the variously ornamented forms of *G. pizcuetana* are:

(a) strongly rounded carinate, turriculate form found at Punfield, BM(NH) GG.21421 (see Fig. 8.1), reminiscent of *turgida* (Zekeli);
(b) more elongate, conical form occurring in the Crackers, BM(NH) G.7810 (see Fig. 7.1; also figured by Arkell, 1947: fig. 37.2); described as *Craginia atherfieldensis* by Mennessier (1984);
(c) very elongate form described initially by Coquand as *C. zekellii*, which is closely similar to *Turritella coalvillensis* Meek (BM(NH) specimen G.76562). We are uncertain (as mentioned above) whether this is an extreme form of *pizcuetana*, or is a separate species of *Craginia*;
(d) another form similar to (a), but with a more pronounced cord and secondary carina in the centre of the adapical shoulder (see De Verneuil & Lorière, 1868: pl. 1, fig. 2c); this has been described as var. *carinata* by Mennessier;
(e) very pagodiform, narrow carinate variety (see De Verneuil & Lorière, 1868: pl. 1, fig. 2b); this has also been included by Mennessier in his var. *carinata*;
(f) coarser, more irregularly ornamented form of carina and spirals figured by Vilanova (1859: pl. 2, fig. 12) from Chert in Spain (see EM 30418; Fig. 9.2).

Genus ***PARAGLAUCONIA*** Steinmann, 1929

1924 *Pleuroceras* (*Pseudoglauconia*) Fritzsche: 35, 37–8; *non* Douvillé 1921.
1929 *Paraglauconia* Steinmann: 112, 113.
1941 *Paraglauconia* Steinmann; Arkell: 101.
1976 *Paraglauconia* Steinmann '1896' [sic]; Akopyan: 138.

Type species. *Paraglauconia carbonaria* (Roemer 1836) [= *Muricites strombiformis* Schlotheim 1820 (*nom. nud.*) and of authors] from the Wealden of Germany (see Arkell, 1941: 101), by subsequent designation of Mennessier (1984: 13) but with incorrect authorship attribution.

Diagnosis and Description. The original diagnosis (Fritzsche, 1924: 38, transl.) stated:

Shell medium-sized, slender, elongate cone-shaped to tower-like. Spiral angle 23–35°, mainly around 30°. Bulky thick shell. Regular whorls ornamented with at least two, or frequently more, smooth or tuberculate [granulate] spiral cords; seldom smooth.

Aperture round to oval; outer lip with 1 or 2 sinuses; inner lip sometimes slightly thickened; apertural margin mostly not continuous. Umbilicus absent or present. Columella usually solid.

The only significant recently published diagnosis is that of Akopyan (1976: 138), which amplified that of Pchelintsev & Korobokov (1960):

Conical, or conical-turreted shell with flattened whorl sides. Ornament principally consists of two strong, cariniform, tuberculate or noded cords, which give the whorls a bi-angular character; other secondary spiral cords may occur. The sinus, situated in the outer lip above the centre of the whorl, is comparatively shallow and not particularly wide.

DISCUSSION. The nomenclature and synonymy of this genus, together with the identification of the various forms of its type species, have occupied the attention of a number of palaeontologists (Rehbinder, 1902: 109–38; Steinmann, 1929: 113; Arkell, 1941: 101–2; Morter, 1978: 22 and Kollmann, 1979: 38). Some of these and other authors have mistakenly considered *Paraglauconia* to be congeneric with *Cassiope*. Initially, the use of the generic name was limited to Purbeck and Wealden forms (see Arkell, 1941 and Morter, 1978). Both Pchelintsev (1953) and Akopyan (1976), however, have assigned later species to the genus. Akopyan mistakenly attributed *Paraglauconia* to Steinmann, 1896, but we have had to assume that this is a bibliographic error, for the genus is not mentioned at all in that paper.

The earlier descriptions need to be amended (see also Kollmann, 1979: 39). The whorls are not always flat-sided; many are concave between the prominent carinae, and others are gently rounded. The carinae are frequently situated close to the sutures and can become extremely pronounced. The sinus in the growth lines occurs either between these carinae, sometimes at that nearest to the centre of the whorl, or occasionally close to the more adapical carina.

Akopyan (1976) first described the distinctive projection of the outer lip shown by the growth lines (see his fig. 4.3) and Kollmann (1979) referred to the ontogenetic changes in shell morphology. Mennessier (1984: 11, 13) recognized two subgenera according to the relative positions of the most anterior 'cordon' and the suture: *Paraglauconia* with 'cordon' at the suture and *Diglauconia* in which the 'cordon' is further away from the suture.

Fritzsche (1924: 35) commented on the various generic assignments ascribed for *Muricites strombiformis* Schlotheim, discussed the morphological differences of cassiopid taxa and concluded that some species belonged to a separate group, which he named *Pseudoglauconia*, designating *P. strombiformis* as its type species. Unfortunately, this name was preoccupied by *Pseudoglauconia* Douvillé 1921. Steinmann (1929: 112, 113) substituted the name *Paraglauconia strombiformis* when recording examples of that species in South America, but did not elaborate upon his reasons for changing the name (see Kollmann, 1979: 38). Steinmann's action was, in effect, the proposal of the new generic name *Paraglauconia* as a replacement for the prior name of *Pseudoglauconia* Fritzsche, *non* Douvillé, but he did not expressly state this as required by I.C.Z.N. Art. 67 (h) (I.T.Z.N. 1985: 125). Therefore, it is not strictly a replacement name and does not automatically take the same type species. Fritzsche's nominated type species *Pseudoglauconia strombiformis* of Schlotheim and authors (1924: 41) is correctly named *Paraglauconia carbonaria* (Roemer) (see p. 257), and is redesignated here as the type species of *Paraglauconia* Steinmann.

Paraglauconia carbonaria (Roemer, 1836)
Figs 10, 11

1820 *Muricites strombiformis* Schlotheim: 144 (*nomen nudum*).
1820 *Muricites turbinatus* Schlotheim: 145 (*non* Brocchi 1814).
1836 *Potamides carbonarius* Roemer: 141 & 216; pl. 11, fig. 17a–b only.
1844 *Potamides carbonarius* Goldfuss: 30 (*pars*); pl. 178, fig. 6d only.
1846 *Melania* (*Muricites*) *strombiformis* (Schlotheim) Dunker: 50; pl. 10, figs 17, 19.
non 1868 *Vicarya strombiformis* De Verneuil & Lorière: 7–10; pl. 1, figs 4a–g (3 different species?)
1870 *Pleuroceras strombiforme* (Schlotheim) Sandberger: 55–56; pl. 2, fig. 11a.
1902 *Glauconia strombiformis* (Schlotheim) Rehbinder: 122 (*pars*).
1909 *Pleuroceras strombiformis* (Schlotheim) Cossmann: 191.

1924 *Pseudoglauconia strombiformis* (Schlotheim) Fritzsche: 41; pl. 2, fig. 9a.
1929 *Paraglauconia strombiformis* (Schlotheim) Steinmann: 112–113, fig. 125.
1941 *Paraglauconia strombiformis* (Schlotheim); Arkell: 102, fig. 54.
1947 *Paraglauconia strombiformis* (Schlotheim); Arkell: 154, text-fig. 35.
1973*b* ?*Procerithium* (*Rhabdocolpus*) *carbonarium* (Roemer) Kemper: 57.
1978 '*Paraglauconia* or *Cassiope strombiformis* (Schlotheim) = *carbonarius* (Roemer)' Morter: 22.
1984 *Paraglauconia* (*Paraglauconia*) *carbonaria* (Goldfuss); Mennessier: 13; pl. 1, figs 4a–d.
1984 *Paraglauconia* (*P.*) *carbonaria nodosa* (Goldfuss); Mennessier: pl. 1, figs 5a–b, 6a–b.

We have not listed all the varietal names of Goldfuss that Mennessier (1984) has raised to species level.

Diagnosis. Conical turriculate shell of medium size. Whorls ornamented by a variable series (dependent on age) of smooth and strongly noded spiral cords. The stronger noded cords occur close to the sutures. Opisthocyrt growth lines cut the cords obliquely and separate the nodes; a deep, narrow, V-shaped sinus occurs at the centre of the whorl side, which is also ornamented by one or more secondary spiral cords.

Syntypes. 1. Material of Schlotheim (1820) attributed by that author to *Muricites strombiformis* and *turbinatus* at the time of publication, from the 'Transitional Limestone' at Bergisch Gladbach and from Neustadt-am-Rübenberge, which are possibly surviving in the collections of the Humboldt Museum, East Berlin.

2. Specimens figured and examined by Roemer in his original publication (1836) including those figured in pl. 11, figs 17a–e (see his p. 216) from the localities quoted: Walderthone, Deister, bei Bückeburg and the type locality of Neustadt-am-Rübenberge. These have not been located in that part of Roemer's collection that has been recovered and curated at the Roemer-Museum in Hildesheim (*fide* Dr Helga Stein, Aug. 1984). However, they do have topotype material from both the Deister and Neustadt localities which may have been labelled by H. Roemer 'sensu F. A. Roemer' (personal communication, Dr M. Kirchner, 1986).

We have also endeavoured to discover whether this material is in the University of Wrocław, Poland, which once had some of Roemer's specimens (see Frech, 1915).

3. The topotype specimen presented by Professor Roemer and identified in his own hand, which the BM(NH) acquired from the Museum of Practical Geology: BM(NH) G.64497. See p. 257.

4. The holotype of *Potamides carbonarius* var. *nodosus* Goldfuss (1844: 28; pl. 173, fig. 6d) from the Berriasian, Clus-bei-Hinden, Lower Saxony, West Germany (in Paläontologisches Institut, Friedrich Wilhelm Universität, Bonn) has been quoted by Mennessier (1984: 13, pl. 1, figs 4a–d) as the holotype of *carbonaria*. However, this is invalid as it was not part of Roemer's type series; Mennessier also misquoted the author of the species.

Material studied. All in the Department of Palaeontology, BM(NH):
G.59 & G.74 (slab); Neustadt, Hannover. Pres'd. B. Bright.
G.64497; Neustadt-am-Rübenberge. Pres'd. Prof. Roemer; see 3 above.
G.685; [? Neustadt]. Purch'd exors Sir P. de M. G. Egerton.
G.51; Neustadt. Purch'd Prof. Morris, 1890.
G.50; Teutoberger Wald. Prof. Morris.
1666; Neustadt-am-Rübenberge. 1679; Teutoberger Wald.
G.64516–26 (11 specimens); Ravensberg, Westphalia. All Mantell coll'n.
GG.21552–4; Ravensberg, Westphalia. Charles Lyell coll'n.
62682 (7 specimens); Teutoberger Wald. Brückmann coll'n.
G.64498 (slab); Hannover.
G.59894 (slab); Hannover. Sowerby coll'n, purch'd 1935.
G.64506–15; Oesede bei Osnabrück. Purch'd Dr A. Krantz.
81789; 81794 (2 specimens); 81793 (4 specimens); 81792 (4 specimens); all from Rehburg, Hannover. Old collection.

Horizon and occurrence. We have added the sources of this material to provide some indication of the reliability of its provenance. Many of these specimens are labelled 'Wealden', a

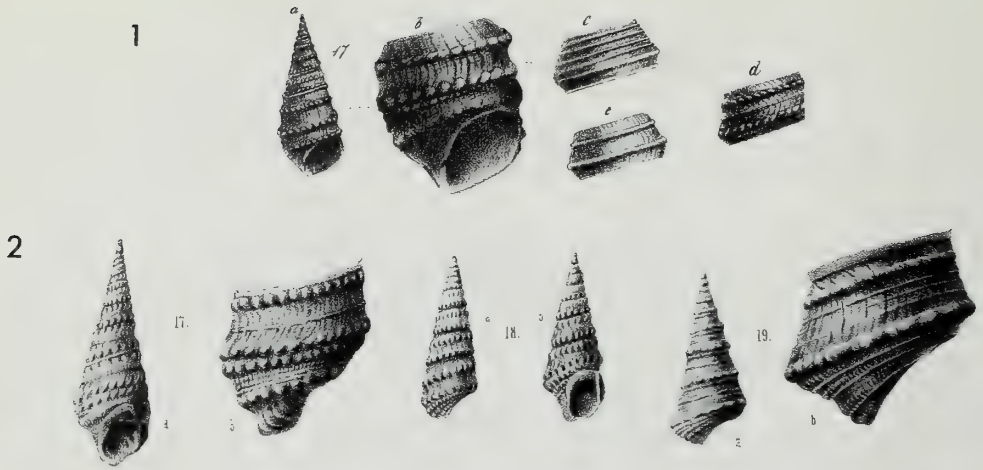

Fig. 10 *Paraglauconia carbonaria* (Roemer, 1836). **1**, original figures of *Potamides carbonarius* given by Roemer (1836); a, b show the typical form according to Roemer and c, d, e provide details of single whorls of several varieties. **2**, original figures of *Melania strombiformis* Schlotheim (*in* Dunker 1846: pl. 10, figs 17–19), respectively showing, according to Dunker, the common form, a more noded variety, and a higher-whorled, less ornamented form.

term that was used to describe a particular German facies which is now regarded as equivalent to the English Purbeckian and has been replaced by the term 'Bückeberg Sequence' (Kemper 1973*a*: 333). In a further paper, Kemper (1973*b*: 52, 57) has recorded the occurrence of *'carbonaria'* with other molluscan species in the Bückerberg Folge 1 [Berriasian 3.1], which comprises the *Cypridea granulosa fasciculata* and *C. granulosa vidrana* Subzones.

Remarks on nomenclature. Although all earlier authors have accepted the designation of *strombiformis* (Schlotheim) as the type species of *Paraglauconia*, the validity of this must be in question. Morter (1978: 22) has pointed out that the name *Muricites strombiformis* Schlotheim is invalid under Article 12, as there is neither 'a description, definition, or indication' as to the identity of this species in Schlotheim's original account (1820: 144–5). The translated description contains nothing that might be regarded as descriptive of this fossil:

From Neustadt in the Rübenberge, Vorharz, and probably from the older formations.... Beautiful specimens, still partly covered by rock in considerable lumps, partly free, apparently completely preserved and preserving the aperture [20 specimens]. This probably belongs to the genus *Cerithium* Lamarck, and up till now has always been cited as a Strombite and has become so known as such that no further description is necessary. It comes from the Rübenberge, in complete petrified shell beds, which consist almost completely of this species of snail. It is subject to some variations. In addition, a variety from Altdorf from the older limestone and a very similar variety from the Müschelflote Limestone of Jena may belong to this species, but both need closer examination in this respect. Perhaps, even the following species, which sometimes occurs mixed with it in the Rübenberge, must also be regarded as a variety.

Consequently, as a *nomen nudum* it is not available. Apparently, Schlotheim considered it to be so well known that further comment was superfluous. His reference to *Muricites turbinatus* Schlotheim and its description might just be considered to comply with the rules. Schlotheim himself thought that *turbinatus* could be a form of *strombiformis*; while both Roemer (1836: 141) and Goldfuss (1844: 30) considered that they were synonyms. We are not aware of any type material of *turbinatus* but *Muricites turbinatus* Schlotheim (1820: 145) is preoccupied by *Murex turbinatus* Brocchi (1814: 443). The specimens of *Muricites turbinatus* from Rübenberge cited by Schlotheim must be regarded as *carbonaria*. We have no knowledge as to the identity of the other specimens from Hard bei Gladbach, listed under *turbinatus* by Schlotheim.

Roemer (1836: 141) replaced Schlotheim's name with the valid synonym *Potamides carbon-*

arius and his illustrations (pl. xi, figs 17a–b only) have been accepted by most subsequent authors as representative of the type of *Muricites strombiformis* Schlotheim; see Dunker (1846: 50), Morter (1978: 22) and Mennessier (1984: 13). The suitability of the name *carbonaria* for the type species is confirmed by a topotype (GG.64497) presented by Professor Roemer; the specimen is accompanied by a label apparently in Roemer's hand and may therefore be regarded as syntypic material. Hitherto authors have continued to use the specific name *strombiformis*, but without having really examined the validity of its nomenclature.

Fritzsche's (1924) original designation of *Pseudoglauconia strombiformis* (Schlotheim) as the type species of his genus was followed by Steinmann's substitution of *Paraglauconia strombiformis* (Schlotheim) in 1929. This and Arkell's acceptance of such designations (1941) are adequate evidence of the use of this combination in palaeontological literature. Consequently, the designation of *Paraglauconia carbonaria* (Roemer) as the type species of the genus is convenient and will not upset the existing concept, for as explained above, Schlotheim's species has been widely accepted as the type species of the genus and this has largely been interpreted upon the basis of Roemer's figures. The subsequent designations of *lujani* Coquand by Pchelintsev (1953: 90) and *lujani* Verneuil by Akopyan (1976: 138) are incorrect as that species was not amongst those listed by either Fritzsche or Steinmann.

Remarks on species. Goldfuss recognized a number of varieties in this species: var. *bilineatus*, var. *multilineata*, var. *trilineata* and var. *nodosa*. Subsequent authors have not consistently accepted or interpreted these. Mennessier (1984) acknowledged that the number of intercalary threads on the flank and base was variable, as well as the number of nodes.

Rehbinder (1902: 122) provided a lengthy synonymy of the Cretaceous literature recording this very variable species. Confusion as to the extent of its variability arises from the inclusion in its synonymy of other quite distinct species. Morter (1978: 22) summarized the history of interpretation of *strombiformis* and has suggested that its varieties—originally described and figured by Goldfuss (1844: 30–31; pl. 173)—should be treated as subspecies. He concluded that the name '*strombiformis*' should only be applied to early Lower Cretaceous (Ryazanian and Valanginian) forms, and that the name was not appropriate for later (Hauterivian and Barremian) gastropods such as those occurring in the Weald Clay, for which he used *Cassiope fittoni* Morter (but see p. 262). De Verneuil & Lorière (1868: 9) had earlier endeavoured to conserve the var. *bilineatus* of Goldfuss as *strombiformis*, yet, as Morter pointed out, this is regarded as synonymous with *Melanopsis tricarinata* J. de C. Sowerby 1836. Arkell (1947: 154) considered var. *nodosus* Goldfuss (his fig. 6d) as the typical form of *strombiformis*, but recognized that it did not occur in England where other forms were more frequent, opinions with which we concur. Mennessier (1984: 13) has raised most of Goldfuss's varieties (*bilineata*, *multilineata*, *nodosa*, *trilineata*) to species level, but retained *nodosa* Goldfuss as a variety of *carbonaria* (Roemer).

Typical *carbonaria*, i.e. the var. *nodosa* of Goldfuss, are not thought to occur in Britain. In our opinion *tricarinata* is closely related, but for the present we have retained it as a separate species (p. 260). The material in the Mantell collection nos 2780–82 (=GG.21560–1; see Fig. 11.2), said to be Wealden, is of doubtful origin, for such preservation is not known at any British locality. Both Arkell (1941) and Morter (1978: 22) have suggested that it might have been collected in NW Germany, as the specimens have considerable similarity with such material. Mennessier has figured these specimens as *Paraglauconia carbonaria nodosa* (Goldfuss) (1984: pl. 1, figs 5, 6). In our view they are closer to the varieties *multilineata* Goldfuss—especially the figure given by Rehbinder (1902: pl. 1, fig. 19)—or *trilineata* Goldfuss, as they possess the much stronger spirals present on the lower part of the whorl that characterize those varieties. However, since it is impossible to separate these Mantell specimens from the example obtained from Pounceford (see Fig. 11.6–8), we are inclined for the moment to regard them as *tricarinata*.

In the Mantell Collection register, held by the Department of Palaeontology, BM(NH), an entry under nos 2765–89 is relevant to the specimens mentioned above. It reads: 'Twenty-five cards, with shells attached some unique and mostly named'. Another general entry relating to

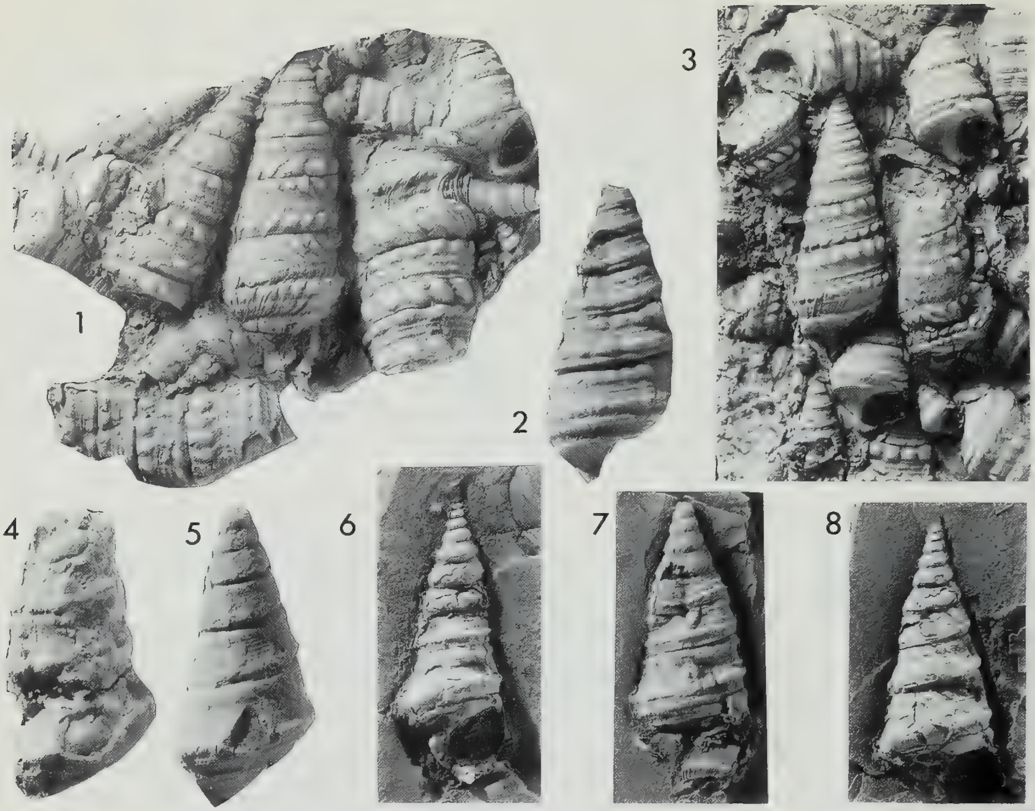

Fig. 11 Species of *Paraglauconia.*

1, 3, *Paraglauconia carbonaria* (F. A. Roemer, 1836). BMNH GG.55365, ? topotype, limestone slab from Neustadt-am-Rubenberge, nr Hannover, West Germany; Wealden (= Berriasian); history unrecorded. 1, area at bottom right of block, × 2; 3, area on opposite side of block, top left, × 1·5.

2, *Paraglauconia* cf. *tricarinata* (J. de C. Sowerby, 1836). BMNH GG.21560, *ex* G. Mantell colln (no. 2780), labelled 'Sussex' but probably from north Germany; × 3.

4-8, *Paraglauconia tricarinata* (J. de C. Sowerby, 1836). 4, OUM J 37550, Corbula Bed, Durlston Bay, Swanage, Dorset. Specimen described by Arkell (1941: 102) as var. *purbeckensis* but figured by him as var. *durlstonensis* (1941: fig. 30); regarded by Mennessier as holotype of *purbeckensis*. Its ornament of fine spirals and tuberculate cords is only just visible; × 3. 5, BMNH G.71007, Corbula Bed, Durlston Bay, Swanage; shows the opisthocyrt growth lines; × 3. 6–8, from Durlston Formn, Pounceford, nr Burwash, East Sussex; all × 2·5. 6, BMNH G.64528, lectotype of *Melanopsis tricarinata*, G. A. Mantell colln. 7, BMNH G.21531, history not recorded; it shows the simple ornament of early whorls in addition to the tubercles, fine spirals and growth lines of the tricarinate later whorls. 8, BMNH G.64529, paralectotype, G. A. Mantell colln.

Mantell's Wealden specimens states: 'This series of Wealden shells etc. has been collected with considerable labor and expense … the specimens being in many instances unique'. This does not necessarily imply the material was personally collected by Mantell—but could merely mean that he acquired it.

Mantell (1847: pl. 6, fig. 5) figured an example of *carbonaria* said to have been collected at Compton Bay in the Isle of Wight. Yet this too is very reminiscent of material from Germany now in the BM(NH) collections (Fig. 11.1, Fig. 11.3).

PRIORITY of *carbonaria* and *tricarinata*. As the descriptions of both species were first published in the same year, 1836, we have endeavoured to ascertain which may have been published first,

in case they should ever be regarded as synonymous. The lists recording the receipt of publications in the principal European geological journals have provided the main evidence.

Bull. Soc. géol. Fr., Paris, **8** (1836–7; Séance 19th Dec. 1836): 64 lists Roemer's *Oolithen-Gebirges*; while in the same journal on p. 406 there is a reference to the *Trans. geol. Soc. Lond.* (2nd Ser.) **4** (2): 103–516, 25 pls (embracing J. de C. Sowerby *in* Fitton, 1836).

Neues Jb. Miner. Geogn. Geol. Petrefakt., Stuttgart, **1836**: 63 lists the first part of Roemer's work; and p. 365 records the second. The bibliographical reference Quenstedt (1963: 21–23) provides a section on Roemer's *Oolithen-Gebirges* in which it indicates that the third part was published in the second half of the year 1836.

John Thackray, of the Geological Museum, BM(NH), after examining the records at the Geological Society of London, has informed us that the earliest acknowledgement of the receipt of the relevant part, as indicated above, of the *Transactions* containing J. de C. Sowerby's descriptions was dated 31st December 1836. This must therefore be the earliest date that can reasonably be attributed to *tricarinata*.

On this evidence we have concluded that Roemer's name of *carbonaria* should take priority.

Paraglauconia tricarinata (J. de C. Sowerby, 1836)
Figs 11, 19

1824	*Melania tricarinata* Fitton: 376 (*nomen nudum*).
1826	*Melania tricarinata* J. de C. Sowerby: 52 (*nomen nudum*).
1836	*Melanopsis ? tricarinata* J. de C. Sowerby *in* Fitton: 228, 346; pl. 22, fig. 4.
1844	*Potamides carbonarius* var. *bilineata* Goldfuss: pl. 173, fig. 6a.
non 1846	*Melanopsis ? tricarinata* Dunker: 51, 85–86; pl. x, figs 16a, b.
1895	*Melanopsis tricarinata* Sow.; Woodward: 366.
1941	*Paraglauconia strombiformis* (Schlotheim) var. *tricarinata* (J. de. C. Sowerby) Arkell: 102.
1941	*'Melanopsis' tricarinata* J. de C. Sowerby; Arkell: 118–120, fig. 53.
1941	*Paraglauconia strombiformis* (Schlotheim) var. *purbeckensis* Arkell: 102.
1941	*Paraglauconia strombiformis* (Schlotheim) var. *durlstonensis* Arkell: fig. 30.
1973*b*	? *Metacerithium* (*?*) *strombiforme* (Schloth.); Kemper: 57.
non 1976	*Pseudomesalia tricarinata* Akopyan: 163; pl. 37, figs 1, 2a, b.
1978	*Cassiope tricarinata* (J. de C. Sowerby) Morter: 21–22.
1984	*Paraglauconia* (*Paraglauconia*) *tricarinata* (J. de C. Sowerby); Mennessier: 16; pl. 1, fig. 45.
1984	*Paraglauconia* (*P.*) *purbeckensis* Mennessier: 13; pl. 1, figs 1–3.
1984	*Cassiope tricarinata* (J. de C. Sowerby); Morter: 219, fig. 5.L.

Diagnosis. Small turriculate, slightly pagodiform cassiopid with three prominent spiral cords, two of which are nodulose, with the first close to the adapical suture; the growth line sinus is in the upper quarter of the whorl side.

Original description (Sowerby *in* Fitton 1836: 346):

Subulate, conical; whorls seven, carinated. Three carinae occupy the exposed portions of the whorls, and are crossed by distinct lines of growth; the central one is the most prominent.

Material and occurrence. In BM(NH): Lectotype, G.64528 (Morter 1978: 21); G.64529; G.67066 [=2744]; 2755; 10857; all G. A. Mantell collection. GG.21531–3; GG.21534–5; GG.21536, history not recorded. All apparently from 'Pounceford', Sussex, which Morter (1984: 218, 227) has given as Purbeck, Durlston Formation, Grays Limestone member (Upper part). See also GG.21560–1 (Fig. 11.2), p. 258. G.71007, Purbeck, *Corbula* Bed; Durlston Bay, Swanage, Dorset. Other questionable, but poorly preserved specimens of *tricarinata* occur on two rock specimens from this bed, L.9804 and L.9807, purchased from the Rev. P. B. Brodie in 1895.

In Oxford University Museum: J 37550, Purbeck, *Corbula* Bed (highest limestone band); Durlston Bay, Dorset; W. J. Arkell collection; holotype of *P.* (*P.*) *purbeckensis* Mennessier and original of Arkell's fig. 30 (1941). This specimen is not as well preserved as Arkell's description implies for little of the shell remains.

In British Geological Survey, Keyworth, Notts.: GSM 75318–9 (and 7 specimens, incl. 80, 26–30), Purbeck, Greys Lst. Member; Burwash Wheel, nr Hastings, Sussex; purchased from H. Butler, 1884. Ca 7959 Geol. Survey 1954 Core: Purbeck, Durlston Formation, Greys Lst. Member; Ashdown No. 1 BH Sussex 1" 303, NGR TQ/5008 3034.

In Sedgwick Museum, Cambridge: J 5585, J 14093.

The species has also been recorded by Woodward (1895: 366) from Dorset and Sussex. Morter (1978: 22) has suggested that this species is probably restricted to the Purbeck beds in England and to the Wealden Bückerberg Formation in Germany (Late Berriasian; see Kemper 1973*a*, *b*).

REMARKS. The poor, slightly squashed preservation of the specimens prevents more precise description and, coupled with the variation in the ornament commonly shown by cassiopids, there is an element of uncertainty in the diagnosis of the species. Mennessier has given a developmental sequence in his description.

The sparsity of *tricarinata* material also leads to difficulty in assessing its characters, which makes any significant comparison with the contemporaneous species *carbonaria* impracticable. For the present, we have retained the name of the British species, for it is possible to discern a number of small differences in shell morphology and ornament. These are summarized below:

	tricarinata	*carbonaria*
(i) whorl shape	bicarinate	tri- to multicarinate
(ii) no. of spirals between main cords	three +	one only
(iii) no. of tubercles &c. on main cords	8, 9, 10	6, 7, 8, 9
(iv) growth line sinus	more opisthocyrt; wide and not too deep	narrow V-shaped and relatively deep
(v) whorl side carinae	nothing between	secondary row of tubercles beneath upper carina
(vi) base	three cords	two cords
(vii) spire/suture	turreted area above suture	noded/tuberculate cords adjacent to suture

However, our acceptance of a wide range of variation in the form of other cassiopid species, e.g. *C. kefersteinii*, *P. lujani* & *G. pizcuetana*, leads to the conjecture that Dunker could be correct in placing *P. tricarinata* in the synonymy of *P. strombiformis* [=*carbonaria*]. It is also difficult to exclude the specimens of *P. purbeckensis* collected from the Corbula Bed at Durlston Bay from the range accommodated under *P. tricarinata*.

Arkell (1941: 120) appears to have been correct in deducing that the original specimen came from the Purbeck exposure at Pounceford rather than the Wealden Shales at Punfield as given by Sowerby. But despite the archival confirmation supporting the identification of the lectotype, the original published figure cannot be said to be an accurate representation of the features of this species; in fact, it bears a greater resemblance to *P. fittoni*. The position of the most adapical primary spiral cord close to the suture serves to separate *tricarinata* from *fittoni*, the spiral cords of the latter are much stronger, while the slight differences in the relative position of the sinus in their growth lines confirms this distinction. The characters mentioned by Morter (1978: 22) are questionable, for apart from that of size, the features attributed to *P. tricarinata* can be readily seen in specimens of *P. fittoni*. Yet, it is probably true that the spiral cords are more numerous, stronger and more nodulose in the former.

Two specimens (G.74558–9) from the Wealden at Osterwald, NW of Hannover, W. Germany have been labelled by Morter as *tricarinata*, but do not appear to possess the same whorl shape or tuberculate ornament of that species. These specimens resemble the juvenile specimen doubtfully referred to *strombiformis* by Dunker (1846: pl. 10, fig. 24), which was subsequently described as *laginensis* by Struckmann (1882: 28). It is possible that they represent an extension of the range of ornament, e.g. *laginensis* → *purbeckensis* → *tricarinata*. Struckmann distinguished *laginensis* from the latter by its vaulted whorls lacking any trace of noded spirals, or keels, but

realised that there were some similarities. (Other examples of this species in the BM(NH) are: 81791 (3 specimens) from Hannover, Old collection; and 63854 from Clus bei Minden, Brückmann collection.)

Paraglauconia shipbornensis (Mennessier, 1984)
Fig. 12

1846 ?*Melania* (*Muricites*) *strombiformis* Dunker: 51 (pars); pl. 10, fig. 18 only.
? 1933 *Glauconia* cf. *lujani* Dines & Edmunds: 38–39.
1947 *Paraglauconia strombiformis* (Schlotheim) var. *mutilineata* Goldfuss; Arkell: 153, fig. 3.
1962 *Paraglauconia strombiformis* (Schlotheim); Castell *et al.*: pl. 61, fig. 3.
1969 *Cassiope strombiformis* (Schlotheim) Dines *et al.*: 34.
1978 *Cassiope* cf. *lujani* (De Verneuil & Collomb); Morter: 21 (pars).
1983 *Cassiope lujani* (Verneuil & Collomb); Castell *et al.*: pl. 61, fig. 3.
1984 *Cassiope shipbornensis* Mennessier: 77; pl. 26, figs 9–10.

Diagnosis. A slender paraglauconid with two prominent spiral cords that have attenuated or elongated nodules/tubercles; a third prominent, less tuberculate, spiral cord occurs towards the base giving a bicarinate appearance to the basal whorl. The tuberculate cords occur adjacent to the impressed sutures.

Material and occurrence. All specimens in the BM(NH). Holotype G.67063 and paratype G.67062; fig'd. Mennessier (1984: pl. 26, figs 9–10). Other material: GG.21537–9; the figure in *British Mesozoic Fossils* (Castell *et al.* 1962: pl. 61, fig. 3) is based on these specimens; Mennessier (1984: 78) included that figure in the synonymy of *Cassiope dorsetensis*. GG.21545–6. All these specimens are from the 'Wealden'; Shipbourne, nr Tonbridge, Kent; they were presented by Mrs Golding in March 1898 (*Ex* G.11039).

From other localities: G.23201, Wealden; Starvecrow, north of Tonbridge, Kent; J. R. Gregory collection, pres'd. 1913. GG.21540–2, Wealden; ? nr Tonbridge; C. T. Trechmann collection. GG.14375, ? Hauterivian, Weald Clay, *Cassiope* band below Sandstone Bed No. 3; southern side [*c.* 1964] of Clockhouse Pit, nr Ockley, Surrey; E. A. Jarzembowski collection. ? Other poorly preserved specimens GG.14365–72 also from Ockley.

Fig. 12 *Paraglauconia shipbornensis* Mennessier, 1984. All from the 'Wealden' (= ? Hauterivian) at Shipbourne, nr Tonbridge, Kent, and presd by Mrs Golding in 1895, when they were registered as a series under G.11309. **1**, drawing of *Paraglauconia 'strombiformis'* (Schlotheim) in *British Mesozoic Fossils* (Castell 1962: pl. 61, fig. 3) based on this series of fossils, now renumbered. **2**, BMNH GG.21539, both ×1·5. **3**, BMNH G.67062, paratype figd by Mennessier (1984: pl. 26, figs 9a, b); left ×1·1, right ×1·3. **4**, BMNH G.67063, holotype figd by Mennessier (1984: pl. 26, figs 10a, b); ×1·1.

LOCALITY AND HORIZON. The stratigraphical relationships of the Weald Clay used here follow Worssam (1978), Dines *et al.* (1969) and C. P. Palmer (personal communication).

All the specimens from the Weald Clay in Kent have an identical imperfect ferruginous preservation which suggests that they could all come from the same horizon, if not the same exposure. The record of *Cassiope strombiformis* (Schlotheim) found at the lower of the two levels of the small *'Paludina'* limestone occurring in an abandoned brickpit (TQ 598495) 450 yds SW of Starvecrow, 2 miles NNE of Tonbridge, published by Abbott (1907: 100; quoted by Dines *et al.*, 1969: 51) indicates the possible source of these specimens. However, the Hauterivian small *'Paludina'* limestone (Topley's (1875) Bed 3) has also been noted in Starvecrow Wood (TQ 597495), 2 miles north of Tonbridge, by Dines *et al.* (1969: 33). Either of these two exposures could represent the original locality, for both are little more than a mile from Shipbourne. Examination of a geological map suggests any other suitable exposure is unlikely. However, the upper horizon of the large *'Paludina'* limestone (Topley's Bed 6), Barremian, has been recorded from Budd's Green, 1 mile west of Shipbourne.

It is possible that the cassiopid identified by Dines & Edmunds (1933: 38) at the same small *'Paludina'* limestone horizon, from a brickyard at Crowhurst (TQ 393464) might also belong to this species. *Cassiope* bands are also known towards the top of Topley's Bed 3, north of Horsham.

The specimens from the Clockhouse Pit, nr Ockley, Surrey, collected from this horizon, were associated with definite marine molluscs: e.g. *Procerithium* sp. (GG.14374) and *Actaeonella* sp. (GG.14373), together with isolated valves of small *Ostrea* sp.

DISCUSSION. Morter (1978: 21) decided that some of the cassiopids found in the Weald Clay were much closer to *'Cassiope' lujani* than to *P. strombiformis*, a view with which we would agree. However, typical forms of *Paraglauconia lujani* occur in the lower Aptian (see p. 266). It is unfortunate that the poor preservation of these eroded specimens prevents either a detailed description or a thorough comparison being made. Examination suggests that their slightly less elaborate ornament is intermediate between *P. strombiformis* and *P. lujani*; its strength is correspondingly greater than that of *strombiformis*, although the nodules/tubercles do not quite attain the same size. The growth lines also reflect this relationship, for although more opisthocyrt and with a deeper sinus than those of *strombiformis*, they are not so irregular or asymmetrical as those of *lujani*. For the present, these specimens are provisionally retained as a separate species. The nature of the ornament and growth lines indicate that it should be placed in the genus *Paraglauconia* rather than in *Cassiope* as believed by its author.

A specimen from the Lower Cretaceous of NW Germany (Dunker 1846: pl. 10, fig. 18) would appear to have the two rows of elongated tubercles occurring in *shipbornensis*.

Paraglauconia fittoni (Morter, 1978)
Fig. 13

1824 *Melania tricarinata* Fitton Ms. (*nomen nudum*).
non 1836 *Melanopsis ? tricarinata* J. de C. Sowerby *in* Fitton: 228.
1846 *Melania tricarinata* Dunker: 51 (*errore*).
1846 *Melania bicarinata* Dunker: descr. pl. x, figs 16 a, b (*non* Grateloup, 1840: 160).
1921 ?*'Glauconia lujani'* Gillet: 34; pl. 3, figs 12–14 (*non* De Verneuil & Collomb, 1853).
1933 *Glauconia* cf. *lujani* (De Verneuil); Dines & Edmunds: 37, 115.
1947 *Paraglauconia strombiformis* var. *tricarinata* J. de C. Sowerby; Arkell: 153.
1971 *Cassiope* sp.; Worssam & Ivimey-Cook: 64.
1978 *Cassiope fittoni* Morter: 21, figs 7, 8, 10.
1978 *Cassiope* cf. *lujani* (De Verneuil & Collomb); Morter: 21, figs 11, 12.
1984 *Paraglauconia* (*Diglauconia*) *fittoni* (Morter) Mennessier: 18; pl. 2, figs 2–3.
1984 *Paraglauconia* (*Diglauconia*) *wassyensis* Mennessier: 22; pl. 3, figs 18–21.
1984 *Paraglauconia* (*Paraglauconia*) *morteri* Mennessier: 14; pl. 1, fig. 15.

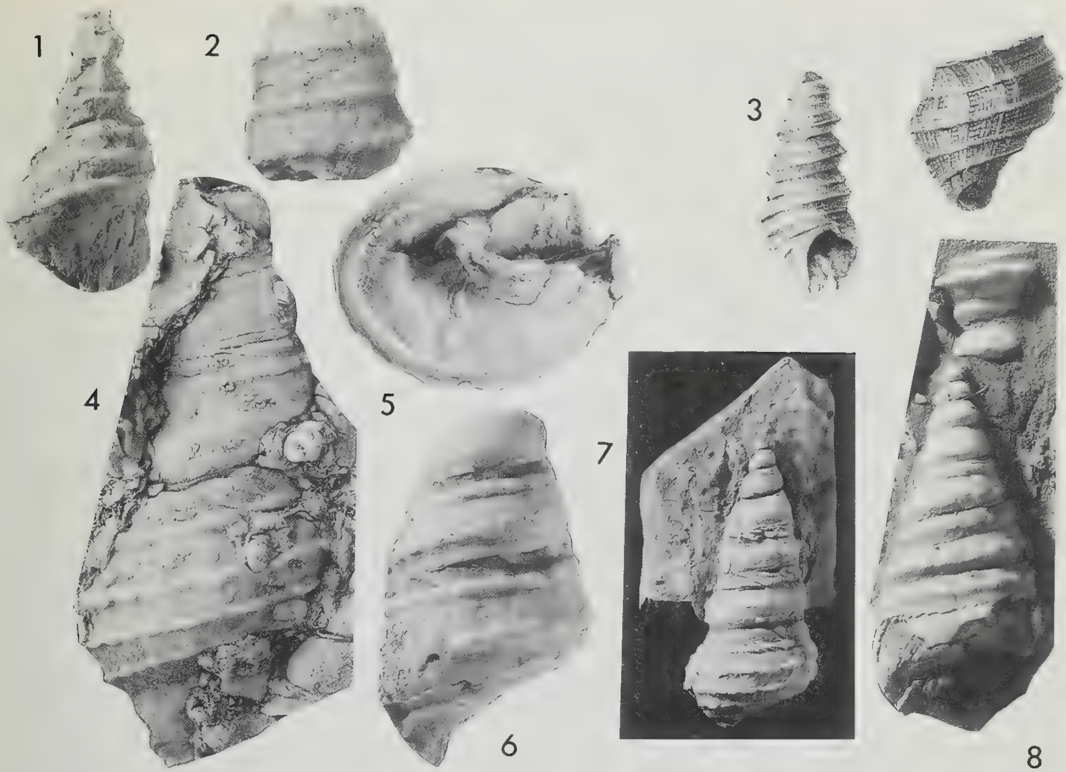

Fig. 13 *Paraglauconia fittoni* (Morter, 1978). **1**, *P.* cf. *fittoni* (Morter). BMNH GG.21320, ×1·5, a specimen extracted from a large limestone block composed of these gastropods; note that the base of the whorl lacks ornament although otherwise the ornament itself is similar to that of *fittoni*. History unrecorded, ? from Germany. **2**, BMNH G.62581, ×4; incomplete shell from the junction of the Weald Clay and the Atherfield Clay (=Barremian) at Earlswood, nr Redhill, Surrey; A. G. Davis colln. **3**, original figures of *Melania bicarinata* Dunker (1846: pl. x, figs 16a, b); from Gravinghagner Stolln, nr Bielefeld, West Germany. **4, 5**, BMNH G.62575, paratype (Morter 1978: fig. 10), from Barremian, junction of Weald Clay and Atherfield Clay, at Brown's Pit, Earlswood, nr Redhill, Surrey; A. G. Davis colln. 4, ×1·5; 5, view of base showing a sinus in the growth lines, ×2 approx. **6**, BMNH G.5316, ×2; 'Wealden', Haslemere, Surrey; F. Harford colln, presd 1889; specimen has ornament similar to *P.* cf. *lujani* (Morter). **7**, IGS GSM.56495, ×1; holotype (Morter 1978: fig. 7), 'Wealden', Sevenoaks, Kent; Caleb Evans colln. **8**, IGS GSM.52045, ×1·5; top of Weald Clay, Haslemere, Surrey; figd as *Cassiope* cf. *lujani* (de Verneuil & Collomb) by Morter (1978: pl. 1, fig. 12); holotype of *Paraglauconia* (*P.*) *morteri* Mennessier (1984: pl. 1, fig. 15).

Diagnosis. Medium-sized, relatively high-spired turriculate cassiopid; ornamented by four significant carinate, slightly tuberculate cords with the most adapical cord situated midway along a ramp; pronounced growth lines on later whorls; sinus between the first and second cords.

Holotype. In BM(NH): 56495, Caleb Evans collection; Weald Clay, Sevenoaks, Kent (Morter 1978: fig. 7). It is assumed from its locality that the holotype came from the highest part of the Weald Clay, which is the only level exposed in the Sevenoaks tunnel that was recorded by Evans (1871: 1–3; Casey 1961: 490).

Material in BGS, Keyworth, Notts.:
Rh 2973; Wealden Shales; Corfe, Dorset; see Arkell (1947: 153) and Morter (1978: 21).
G Sd 3777; Wealden Shales; Punfield, nr Swanage, Dorset.
Geol. Soc. coll'n 2346 & 2614; Wealden Shales; Atherfield, I.o.W.

BDN 5340, 5342, 5345, 5347, 5349; top of Weald Clay, *Cassiope* bed; from borehole at Huilands Farm, Sussex (Barremian).

52045 (Morter 1978: fig. 12); Barremian, top of Weald Clay; Haslemere, Surrey (Topley Bed 11). See Thurrell *et al.* (1968: 20); this is from the uppermost Weald Clay formerly exposed in the railway cutting at Haslemere (cf. Topley 1875: 114).

Zr 7350 (Morter 1978: fig. 11); Local Bed 5, Lower *Cyrena* limestone; Warnham Brickworks Pit, Warnham, Sussex (Barremian).

Material in BM(NH):

Paratypes G.62575 (Morter 1978: fig. 10) and G.62576–81; A. G. Davis collection from the junction of the Wealden and Atherfield Clay at Brown's Pit, Earlswood, nr Redhill, Surrey (Barremian; see Dines & Edmunds (1933: 37, 115) on locality).

G5316 (3 specimens), F. Harford collection 1889; Wealden; Haslemere, Surrey (? Barremian, Bed 7 upwards, see note above regarding locality).

G.61019, A. G. Davis collection; ironstone nodules within 7 ft of top of Weald Clay (? = Topley Bed 11, Upper Barremian); Earlswood, Surrey.

Morter considered that this species was common in the *Cassiope* beds of the Weald Clay and Wealden Shales. Concurring with this, we would further suggest that *fittoni* occurs in the Upper Barremian throughout Europe. Although Dunker (1846) recorded specimens that are now included in this species as having been found very sporadically with *P. strombiformis* at Gravinghagner Stolln, nr Bielefeld, Germany, we are skeptical that the two were associated, or occurred at the same horizon.

Discussion. The greater size of *fittoni* has been an adequate character for separating it from other Lower Cretaceous cassiopids. However, it must be remembered that in comparison with later species it cannot be considered 'large'.

There is no need to add to the detailed description given by Morter. But it is worthwhile emphasizing that the majority of the British specimens are crushed and often eroded; that his reference to basal ornament is questionable; and that his suggestion that the outer lip could possibly have been extended into a wing is extremely unlikely for we have seen no evidence of this. The condition of the material probably contributed to the fact that associated cassiopids were described as *P.* cf. *lujani*. But closer examination has established that the same degree, i.e. frequency and nature, of tuberculate ornament occurs on the cords of all specimens, and that acknowledged *P. fittoni* material also has identical juvenile whorls and other features in common. It would appear that the 'profound furrow' described as a feature of Mennessier's (1984) *P. morteri* is a result of crushing. The characteristic ornament on the spiral cords is perhaps best described as being between the author's 'weakly developed tubercles' and Mennessier's 'nodules allongés'; it is also undoubtedly influenced by the growth lines. The nature of the ornament on the cords separates *P. fittoni* from both *P. lujani* and *P.* cf. *frechi*. The bicarinate, straight-sided mid-whorl section seems to distinguish this species from other British cassiopids, particularly the broader Aptian shell *P.* cf. *frechi*. Occasionally a second sinus can be seen on the base close to the aperture. As mentioned above, the position of the most adapical cord away from the suture assists in distinguishing *P. fittoni* from *P. tricarinata*; this feature would also place the species in Mennessier's subgenus *Diglauconia*.

Dunker obviously recognized Sowerby's name *tricarinata*, for he included it in the synonymy of *strombiformis*. His re-use of the name is obviously in error for he corrected it by substituting *bicarinata* in the plate description. On the basis of his figure and description, we cannot see any distinction between Dunker's species and *P. fittoni*. The name *Melania bicarinata*, however, is preoccupied by Grateloup's earlier use for a Recent gastropod from Madagascar.

Morter (1978: 21) suggested that the specimens from the Upper Barremian at Wassy (Haute Marne) figured by Gillet (1921: pl. 3, figs 12–14) as *Glauconia lujani* should probably be included in *P. fittoni*. Gillet (1921: 35) had realised that the Wassy material did not correspond with the figure of *lujani* given by Peron (1899), but had concluded that the French specimens were juveniles and similar to specimens figured by De Verneuil & Lorière (1868: figs 3e, 3h).

Paraglauconia lujani (De Verneuil & Collomb, 1853)
Fig. 14

1853 *Cerithium lujani* De Verneuil & Collomb: 102, 165–166; pl. 3, fig. 17.
1854 *Cerithium heeri* Pictet & Renevier: 51, 171; pl. 5, fig. 4.
1859 *Cerithium luxani* Vilanova: pl. 3, fig. 7 (unjustifiable emend.).
1863 '*Vycaria luxani* Verneuil' (*sic*); Vilanova: pl. 5, fig. 19.
1866 *Cassiope lujani* (De Verneuil & Collomb) Coquand: 251–252; pl. 4, figs 3–5.
1866 *Cassiope verneuilli* Coquand: 251; pl. 4, figs 1–2.
1868 *Vicarya lujani* (De Verneuil & Collomb) De Verneuil & Lorière: 5–7; pl. 1, fig. 3.
1899 *Glauconia* cf. *lujani* (De Verneuil) Peron: 95–96; pl. 1, fig. 10.
1909 *Glauconia lujani* (De Verneuil); Cossmann: pl. 4, figs 11–12.
1947 *Cassiope lujani* (De Verneuil & Collomb); Arkell: 168, fig. 37.6.
1947 *Cassiope lujani* var. *crassa* Arkell: 168, fig. 37.3.
1976 *Paraglauconia lujani* (Verneuil) Akopyan: 138.
non 1978 *Cassiope* cf. *lujani* (Verneuil & Collomb); Morter: 21; pl. 1, fig. 12.
1984 *Paraglauconia lujani* (De Verneuil & Collomb); Cleevely *et al.*: 98; fig. 2, nos 11–14.
1984 *Cassiope dorsetensis* Mennessier: 78; pl. 27, figs 10 & 11.
1984 *Cassiope luxani* (De Verneuil) *emend.*; Mennessier: 78; pl. 26, figs 17–27; pl. 27, fig. 6.
1984 *Cassiope luxani* (De Verneuil) *nodosa* Coquand; Mennessier: 78; pl. 26, fig. 27a, b.
1984 *Cassiope luxani* (De Verneuil) *crassa* Coquand; Mennessier: 78; pl. 27, figs 4–5.

Diagnosis. A variably-ornamented, small to medium-sized cassiopid, characterized by the occurrence of a strongly noded or tuberculate spiral cord at each of the sutures; the sinus in the opisthocyrt growth lines occurs between these cords in the upper third of the whorl.

Syntypes. Three specimens, EM 30409–11, from Utrillas, Teruel in the De Verneuil collection, École des Mines, Paris (at present (1983) in the Département des Sciences de la Terre, Lyon); and three specimens, GG.20928–9, presented by De Verneuil in 1854 to British Museum (Natural History). The locality of the specimen originally figured (1853) was given as 'dans les couches ligniteuses de la Venta de la Mina près Siete Aguas entre Requena et Bunol', but this has not been identified.

Material from Spain. Cretaceous:

In École des Mines, Paris (at Lyon, as above): EM 30401–8; EM 30412–16, Coquand coll'n, from Utrillas.

In BM(NH): 46320, two specimens purchased from M. J. Rothschild in 1864.

In Magyar Állami Földtani Intêzet., Budapest: K 3228 (4), K 3231 from Arcaine; K 3227, K 3230 from Utrillas/Aliaga. These specimens were only examined by photographs.

Material from Britain. Punfield Marine Band:

In BM(NH): GG.21382, GG.60848, GG.9338–44, GG.21410 (3 specimens), GG.21415 (4 specimens); all from Punfield Cove, nr Swanage, Dorset.

In BGS: 70314, Worbarrow Bay, Dorset; 70315, Corfe Castle, Dorset, the holotype of *Cassiope dorsetensis* Mennessier.

Further occurrences. Coquand (1866: 252) recorded this species from 16 Cretaceous localities in Spain. Despite his comment that the species appeared to be associated with lignitiferous deposits, faunal lists compiled from his monograph would suggest that the species occurred in marine conditions. However, there is no definite evidence available in the literature as to the precise horizons at which the species is found.

Discussion. This species has been adequately described by De Verneuil & Collomb (1853), Coquand (1866) and De Verneuil & Lorière (1868). Coquand distinguished several varieties amongst the specimens found in Spain on the nature of their shell shape and strength of ornament. Unfortunately, none of these extreme forms can be recognized with any certainty amongst the material preserved in the Coquand collection at Budapest. It is possible that the originals of var. *laevigata* (K 3230) and var. *nodosa* (K 3231) have survived, but none of Coquand's labels exist to substantiate this. Two differently ornamented forms were also recog-

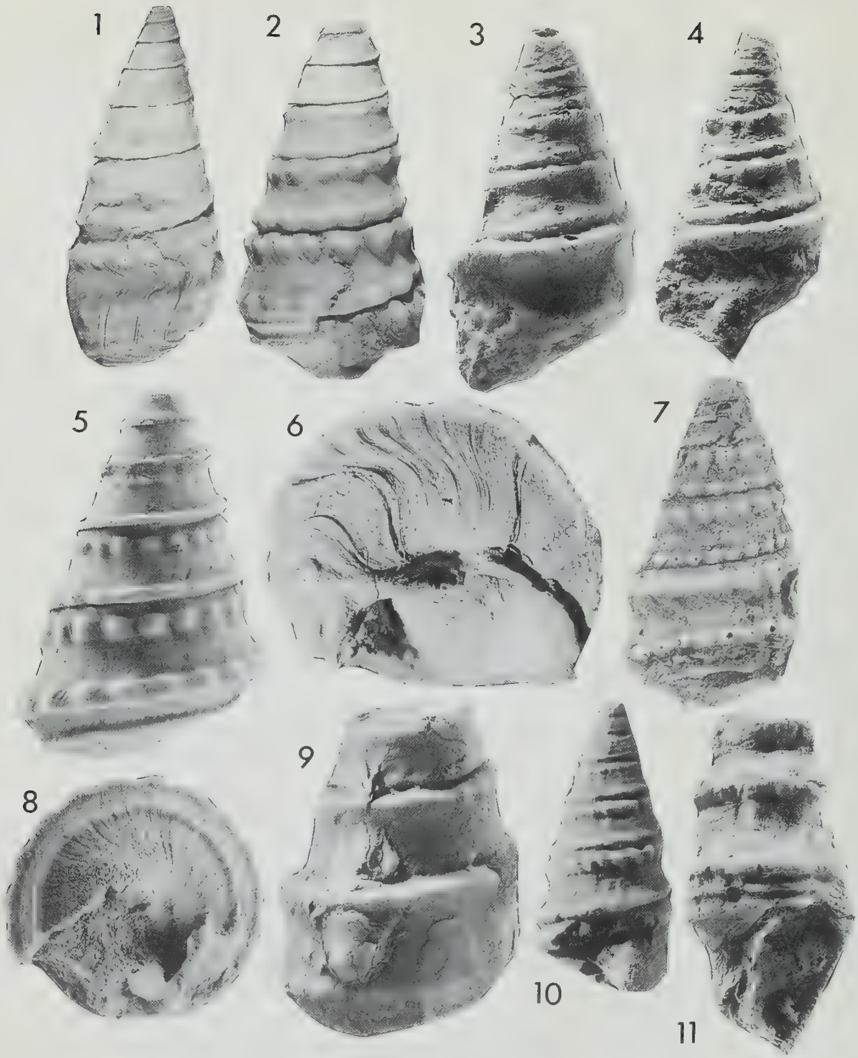

Fig. 14 *Paraglauconia lujani* (De Verneuil & Collomb, 1853); the specimens prefixed EM are at Lyon (see text). **1**, EM 30401, ×2 approx.; Utrillas, Spain; Coquand colln. **2**, EM 30411, ×1·5; Utrillas, Spain, De Verneuil colln; ? syntype of var. *laevigata*. **3**, BMNH GG.21409,. ×1·5; Punfield Marine Band, Punfield, nr Swanage, Dorset; ? = var. *crassa*. **4**, BMNH GG.21410, ×1; Punfield Marine Band, Punfield, Dorset; poorly preserved specimen but showing typical noded cords on either side of a grooved suture. **5, 8**, BMNH GG.20928, ×2·5; Teruel, Spain; one of three syntypes presented by De Verneuil, 1854. **6**, EM 30410, ×4; Utrillas, Spain; De Verneuil colln; ? syntype; basal view showing gradual increase with maturity in the depth of second sinus. **7**, IGS 70314, ×1·3; silicone rubber mould from the paratype of *Cassiope dorsetensis* Mennessier (1984: pl. 27, figs 10, 11). **9**, BMNH GG.9344, ×2; Punfield Marine Band, Punfield, Dorset; fragment encrusted with small oysters. **10**, BMNH GG.21811, ×2·5; *Paraglauconia* sp. nov.?; Tithonian, nr Sa'ana, N. Yemen. See p. 239. **11**, BMNH GG.21382, ×1·5 approx.; Punfield Marine Band, Punfield, Dorset; showing basal whorl and trace of aperture.

nized by De Verneuil & Lorière at Utrillas, where each was considered to be characteristic of a particular horizon, but we have been unable to discover any subsequent work in confirmation.

Coquand considered that the specimen first figured as *lujani* by De Verneuil & Collomb (1853), that called *luxani* by Vilanova (1859, 1863), and that described as *heeri* by Pictet & Renevier (1854), were all examples of his *Cassiope lujani* var. *laevigata*. However, in 1868, De Verneuil & Lorière maintained that *heeri* and *lujani* were quite distinct from one another as the tuberculate cords were in the centre of the whorl in the first species and close to the sutures in the second. *Cassiope picteti* Coquand (1865: 253; pl. 4, figs 6–7) was distinguished by having a very slender shell, although its ornament of median tuberculate cords would suggest a close affinity to *lujani*. De Verneuil & Lorière (1868: 8) mistakenly synonymized both *picteti* and *heeri* with *Muricites strombiformis* (Schlotheim, 1820), a synonym of the type species of *Paraglauconia* Steinmann. Peron (1889: 50; pl. 19, fig. 18), in identifying a Tunisian fossil as *picteti* Coquand, and recognizing *lujani*, *heeri* and *picteti* as separate species, has confused the matter further.

Arkell (1947: fig. 37.3) described Aptian material from Worbarrow as var. *crassa* Coquand; this is considered to be the new species *Cassiope dorsetensis* by Mennessier (1984: 78). A number of the specimens from Punfield, e.g. GG.21415, GG.21382 and GG.9343, also have the turreted form and very pronounced adapical carina on their later whorls characteristic of this form. Several other specimens are comparable to the earlier whorls of the var. *nodosa*, yet none of these have the gross proportions in shell form that Coquand believed were another feature of this variety. Not one of the Punfield specimens could be described as elongate, but several, e.g. GG.9341, possess the weaker ornament and less marked suture ascribed to Coquand's var. *laevigata*. Although the preservation of the Punfield Marine Band specimens is not good, they do show a wide range of ornament which does not conform to the features shown in the varieties described by Coquand. Without an extensive series to determine their range of ornament variation, we suspect that they are all forms of *P. lujani*. The more typical ornament of *P.*

Fig. 15 *Mesoglauconia* from Lebanon.

1, 2, *Mesoglauconia ? frechi* (Blanckenhorn, 1890). BMNH G.19481, Lower Cretaceous, from Kielay, Lebanon; Fahid colln, purchd from Rev. C. Gollmer, 1907. 1, × 1·1; 2, × 1·5, shows growth lines.

3, *Mesoglauconia frechi* (Blanckenhorn, 1890). BMNH G.19472, × 1·25; Lower Cretaceous from Beuah, Lebanon; shows sutural shelf and growth line trace.

4, 5, *Mesoglauconia bicarinata* (Hamlin, 1884). Lower Cretaceous, Aptian, from 'Olive' locality nr Abeih, Lebanon; R. Damon colln, 1878. 4, BMNH GG.14377; 5, GG.14378; both × 1·5.

lujani, with tuberculate or noded cords at the sutures, together with opisthocyrt growth lines having a sinus occurring between the cords, is well illustrated by the Spanish specimens (Fig. 14.5) and by Arkell (1947: fig. 37.6).

Without extending our comparison much further, we would consider that *Glauconia abeihensis* Fraas, figured by Blanckenhorn (1890: pl. 7, fig. 17a–c) from the Aptian at Abeih, Lebanon, and *Cassiope branneri* (Hill), figured by Stanton (1947: pl. 57, figs 1–6) from the Commanche Series (L. Cretaceous) of Glen Rose, near Granbury, Texas, were other close relatives of *P. lujani.*

Morter (1978: 21; pl. 1, figs 11–12) has described a Wealden form, from localities in Sussex and Surrey, as *Cassiope* cf. *lujani*; he also ascribed comparable specimens from the Hauterivian of Saintes-en-Puisaye, France (Peron 1899: 95–96) to the same species. Gillet (1921: 34–35; pl. 3, figs 12–14) described material from the Upper Barremian 'Couche Rouge' at Wassy, Haute Marne, as *Glauconia lujani* (de Verneuil), although she realised that the specimens did not correspond to typical forms. As explained above (p. 264) we do not consider that these are *P. lujani*, their ornament being less tuberculate, and the spirals arranged differently from any recognized forms of that species. Furthermore the pattern of the growth lines is quite different, and the sinus occurs much higher on the whorl; these have been included in *Paraglauconia fittoni* (Morter) described above.

Genus ***MESOGLAUCONIA*** Mennessier, 1984

1984 *Mesoglauconia* Mennessier: 27.

Type species. *Mesoglauconia renevieri* (Coquand 1865), by original designation.

Diagnosis. The original diagnosis (Mennessier 1984: 27, transl.) is as follows:

Conical turriculate shell, holostomatous, of medium size, rarely slightly pupoid; apical angle varies from 36° to 48°; columella smooth; linear suture; last whorl continues slightly obliquely.

Sinuous growth lines [generally there is a wide shallow sinus in centre of whorl side, which is in upper two-thirds of whorl—R.J.C.]: 'point of tangence' between the [first] third and the centre; point of inflexion between the posterior third and quarter; straight on the base, sometimes convex toward the front.

Ornament on young whorls composed in general of two smooth or nodulose principal cords, [one] against the anterior suture and [the other] at the posterior third, or an anterior sutural cord and some threads. Ornament of later whorls is formed by two smooth or nodulose principal cords, [one] against the anterior suture and [the other] at the posterior third, with sometimes a cord or swollen collar against the posterior suture.

Base ornamented by two to four smooth or nodulose peripheral cords.

Discussion. Mennessier (1984: 11) divided this genus into two sub-genera, *Mesoglauconia* (*Mesoglauconia*) with narrow cords, and *Mesoglauconia* (*Triglauconia*) with strongly nodulose cords. He described their general form as being rather squat. Two or three cords were present in both the young and adult shells and the ornament altered slightly with growth. The species that Mennessier has assigned to *Mesoglauconia* (*Mesoglauconia*) appear to form a natural group, for we had recognized the same relationship quite independently.

The most characteristic features of the genus are the combination of a wide shell having a large apical angle with simple ornament composed of regularly-spaced, strong, narrow spiral cords. The strength and position of these cords is variable and this probably reflects specific differences. Another variable feature is the relative position of the sutures and spiral cords, which is particularly noticeable at the adapical suture where the whorl may have a rounded shoulder (*renevieri*), a narrow rim (*frechi*), a concave shelf (*frechi*), a sloping ledge (*bicarinata*), or be adpressed against the preceding whorl (*arkelli* and *studeri* var.). The suture itself ranges from being adpressed to impressed, or even grooved. However, these differences could also merely represent variation within a single species.

The Japanese Lower Cretaceous cassiopids have a similar morphological range and Kobayashi & Suzuki (1939: 223) referred them all to *'Glauconia' neumayri* Nagao. However, Kase

(1984) described them as separate species of *Cassiope* on the basis of their shell morphology and apertural features, and their occurrence at different stratigraphical horizons. The ornament of *C. sebayashiensis* Kase is composed of closely-packed, fine, wavy secondary spirals and smooth

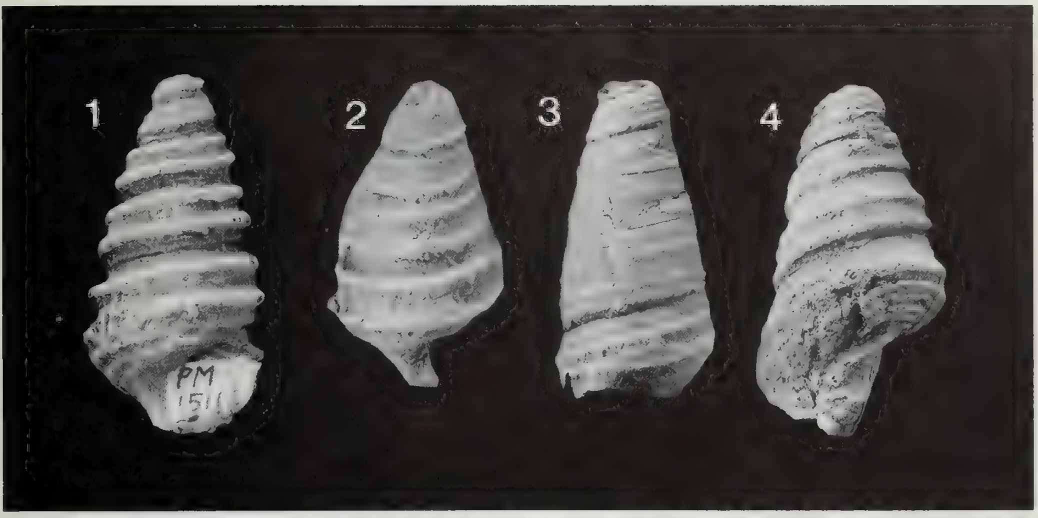

Fig. 16 Cretaceous *Mesoglauconia* and *Cassiopella* species from Japan. All specimens in the colln of National Science Museum, Tokyo.
1, 2, from Kawaguchi Formation, Yatsushiro area, S.W. Japan. 1, *M. neumayri* (Nagao, 1927), Hauterivian–Barremian. PM 15112, × 1·5. 2, *M. angusta* (Kobayashi & Suzuki, 1939), Barremian. PM 15193, × 1·4.
3, 4, from Sebayashi Formation. 3, *M. sebayashiensis* (Kase, 1984), Aptian, from Sanchu area, N.E. Japan. Note wide sinus in growth lines characteristic of *Mesoglauconia*. PM 15122, × 1. 4, *Cassiopella ogaii* Kase, 1984, replica of holotype from Sebayashi, N.E. Japan. Note slight notch in aperture and columella snout. PM 15234, × 1.

Fig. 17 Forms of *Mesoglauconia studeri* from Spain. **1**, *M.* cf. *studeri* (Vilanova, 1863). BMNH 70208, × 3; Mirambel, Spain; presd Prof. J. Vilanova, 1869. **2**, *M. studeri* (Vilanova, 1863), var. BMNH GG.21557, × 2; Benural, Spain; purchd from M. J. Rothschild, 1864. **3**, *M.* cf. *studeri* (Vilanova, 1863). BMNH GG.21556, × 2; Benural, Spain; purchd from M. J. Rothschild, 1864.

primary cords, but the wide sinus in its growth lines confirms that it belongs to *Mesoglauconia*. For the present, we are also treating the Lebanese mesoglauconids as separate species.

From a detailed examination of shell ornament in the Japanese specimens Kobayashi & Suzuki (1939) recognized that one of the principal differences between them was the extent to which the whorls 'embraced each other'. The nature of the suture and the height of individual whorls are effects of this. It is possible some change in the generative curve may have been the cause, but the most likely explanation would seem to be a gradual decrease in the translation rate of shell growth, with consequent increase in whorl overlap (Raup 1966). This would provide the gastropod with an alternative method of increasing shell strength and therefore have a definite functional advantage, for example in order to occupy other marine habitats where it was advantageous to have a stronger shell. However, such a change in shell shape would also have affected its speed of locomotion (Linsley 1978). The converse situation also occurs in the adult stage of several other species of cassiopids: for instance in *Gymnentome pizcuetana* the translation rate increases, the last whorl overlaps to a lesser extent and the shell coiling becomes less regular.

List of species. Mennessier placed nineteen species in his genus. In addition to the six species he included in the subgenus *Mesoglauconia* (*Mesoglauconia*) we would add those marked + in the list below:

	**renevieri* (Coquand) [type sp.]	Lr Aptian	Spain & U.K.
?	**grata* (Mennessier)	Hauterivian–Barremian	Spain
	**studeri* (Vilanova)	Lr Aptian	Spain
	**bicarinata* (Hamlin)	Lr Aptian	Lebanon
	+*frechi* (Blanckenhorn)	Aptian	Lebanon
?	*subseetzeni* (Blanckenhorn)	? Albian	Lebanon
?	*syriaca* (Mennessier), *non* Frech	Lr Aptian	Lebanon
	**arkelli* Mennessier	Aptian	U.K.
	+*neumayri* (Nagao)	Hauterivian–Barremian	Japan
	+*angusta* (Kobayashi & Suzuki)	Barremian	Japan
	+*sebayashiensis* (Kase)	Aptian	Japan
	**burnsi* (Stanton)	Lr Albian	Texas
?	*reyi* (Mennessier)	Barremian	Portugal
?	*angoliensis* (Mennessier)	Aptian	Angola

* = species originally included by Mennessier (1984)
\+ = species added here
? = species doubtfully included

Mesoglauconia renevieri (Coquand, 1865)
Figs 18.1–4, 6

1865 *Cassiope renevieri* Coquand: 254; pl. 4, fig. 8.
1868 *Vycaria studeri* Vilanova (*pars*): descr., pl. 5, fig. 18 only.
1909 *Glauconia renevieri* (Coquand) Cossmann: 168 (name in list only).
1941 *Terebralia* (*Pyrazisinus*) *renevieri* (Coquand) Delpey: 44 (name only).
1949 *Glauconia renevieri* (Coquand); Bataller: 67–68, fig. (copy of Coquand).
1984 *Mesoglauconia* (*Mesoglauconia*) *renevieri* (Coquand) Mennessier: 28; pl. 4, fig. 1a, ? figs 2–4.
1984 *Mesoglauconia* (*Mesoglauconia*) *studeri* (Vilanova) Mennessier: 27; pl. 3, fig. 50 (copy of original figure).
1984 *? Paraglauconia* cf. *frechii* (Blanckenhorn); Cleevely *et al.*: 96, fig. 2.

Amended diagnosis. Cassiopid with slightly tiered, flattish-sided whorls, ornamented by a series of regularly-spaced spiral cords that can be tuberculate or nodose, but are generally narrow, smooth and carinate.

Type material. The original of Coquand's (1865) figure is presumably with the remains of his collection in Budapest, but the only possible syntype (K 3179 from Josa, Teruel) we have been able to trace at Budapest does not appear to be the specimen figured in his pl. 4, fig. 8. This was a well-preserved example presumably obtained from Morella (Castellón), as that was the

only locality quoted. Mennessier (1984: 28) figured as neotype a specimen from the type locality, belonging to the De Verneuil collection; this is probably at Lyon, but no details were given.

Material studied & occurrence. Spain: BM(NH) GG.21555 (*ex* 46029) purchased from M. J. Rothschild, 1864; GG.21559 & 70203, presented by Prof. J. Vilanova in August 1869; all from Benural, Teruel. Coquand recorded this species from both Chert and Morella (Castellón); Vilanova's type came from Aliaga (Teruel); Mennessier's figured material was from Zorita-del-Maestrazgo, Teruel, Dr S. Calzada coll'n.

Britain: BM(NH) GG.21411–2, Martin Simpson coll'n; GG.21380 & GG.9345, G. Bate & R. J. Cleevely coll'n; all from the Punfield Marine Band, Aptian, *Forbesi* Zone, Punfield Cove, nr Swanage, Dorset. All the British specimens are poorly preserved and are internal moulds with fragments of shell preserved. When the shell has been preserved (as in GG.21411–2) it has been worn almost smooth and become pitted with numerous microscopic borings; in all cases the growth lines are not very clear.

Lebanon: BM(NH) G.19496, an internal mould from Duccan probably belongs to this species.

Revised description. Medium-sized turriculate cassiopid; its whorls may be tiered or slightly convex. Variably ornamented by several regularly-spaced spiral cords, the upper ones often slightly tuberculate or nodose, while those on the lower half of the whorl are much narrower and sharper. A rounded shoulder occurs at the adapical suture, although the frequent, irregular serrations made by the growth lines give a strong cord-like appearance and often make it the most prominent ornamental feature. This 'adapical cord' may be as strong or stronger than the others, and contributes to a flatter-sided whorl. Mennessier described the shell as being slightly tiered ('légèrement étagés'). The sinus of the asymmetrical opisthocyrt growth lines occurs at the first true spiral cord, which is some distance from the adapical suture. In some instances this sinus may be quite sharp, narrow and v-like, but it is generally much wider and consequently gentler.

Discussion. An element of uncertainty exists over our interpretation of *renevieri*, for although the specimens available to us appear to conform with the figures of Coquand (1865: pl. 4, fig. 8) and Mennessier (1984: pl. 4, fig. 1a), the description of both those authors mentions the species as having a short or squat form. Yet, in our opinion, this cassiopid is reasonably high-spired, even if not comparable to the size of *G. pizcuetana* and other later species of *Gymnentome*.

The specimen figured by Vilanova (1863: pl. 5, fig. 18) as *'Vycaria' studeri* (which is the type of that species!) is very close to the Spanish material we have identified as *renevieri*. Vilanova considered that his other specimens from different localities, and perhaps from different stratigraphical horizons, were varieties of *studeri*.

A further discrepancy occurs in the shape of the growth lines that various authors have depicted. Coquand's single figure shows rather stylized sigmoidal/parasigmoidal growth lines without any true cassiopid sinus. In Mennessier's 'neotype' they have an opisthocyrt-like shape with a wide shallow sinus. Our Spanish material ranges from forms in which they have a slightly more angular opisthocyrt shape to others having a very narrow v-like channel in the centre.

From a superficial resemblance of growth-line and ornamental characters, Delpey (1941: 44) suggested that the Cassiopidae were related to the Turritellidae. However, she believed that *renevieri* lacked the characteristic cassiopid sinus and, in our opinion, incorrectly assigned it to *Terebralia* (*Pyrazsinus*).

Mesoglauconia (Mesoglauconia) arkelli Mennessier, 1984

Fig. 18.5

1947 *Cassiope pizcuetana* (Vilanova) var. cf. *renevieri* Coquand; Arkell: 168, fig. 37.1 (*non* Coquand, 1865: 254)

1984 *Mesoglauconia* (*Mesoglauconia*) *arkelli* Mennessier: 27; pl. 3, fig. 46.

Diagnosis. Cords narrow, the anterior cord away from the suture.

Fig. 18 Species of *Mesoglauconia*.
1–4, 6, *Mesoglauconia renevieri* (Coquand, 1865). 1, 2, BMNH GG.21411, Punfield Marine Band, Punfield Cove, Dorset; Martin Simpson colln; 1, ×1·5; 2, ×1. Note convex whorls, adpressed sutures, slight rounded adapical shoulder, and the presence of two spiral cords on all but last whorl, the most adapical of which is very slightly tuberculate. 3, BMNH GG.21559, ×1·5, from Benural (Teruel), Spain; Vilanova colln. 4, BMNH GG.21555 (*ex* 46029), ×1 approx.; from Benural, Spain; purchd from M. J. Rothschild, 1864. Note the narrow sinus in growth lines. 6, BMNH GG.21380, ×2; Punfield Marine Band, shore at Punfield Cove, nr Swanage, Dorset; colld G. Bate & R. J. Cleevely.
5, *Mesoglauconia arkelli* Mennessier, 1984. Holotype, IGS GSM.70317, ×2; Punfield Beds, Goods Yard, Corfe Castle, Dorset.

Holotype. BGS GSM70317, from Goods Yard, Corfe Castle, Dorset. This is the badly squashed specimen originally figured by Arkell (1947).

Original description. Turriculate holostomatous shell of medium size; whorls slightly convex; linear suture; entire columella; last whorl continues obliquely. Sinuous growth lines: point of tangence in the anterior third; point of inflexion in posterior third. [In the holotype] early whorls destroyed. From the third whorl ornament consists of three smooth narrow cords: the anterior and weakest in the most anterior quarter; the central and the strongest in the posterior third; the posterior one against the suture. Base not preserved. (Mennessier 1984: 27, transl.).

Discussion. The holotype is fragmentary, and unfortunately the growth lines have not been preserved. Its slightly convex whorls and the position of its most adapical cord away from the suture provide some distinguishing features and serve to separate it from *renevieri*. The repre-

sentations of an axial element in figures of this specimen are based on an artefact of preservation. Its ornament and slightly convex whorls suggest a close affinity with some of the specimens figured as *'Vycaria' studeri* var. (Vilanova 1863: pl. 5, fig. 20; Mennessier 1984: pl. 3, fig. 48).

The Japanese species *'Cassiope' neumayri* (Nagao, *in* Yabe 1927) has a similar adapical shell, but the disposition of its spiral cords and their strength are quite different and much closer to the Lebanese cassiopids referred to below.

Occurrence. Corfe Castle near Swanage, Dorset.

Mesoglauconia frechi (Blanckenhorn, 1890)
Fig. 15.3

1890 *Glauconia Frechi* Blanckenhorn: 101; pl. 7, fig. 16 (fig. 10 on plate).
1927 *Eunema? bicarinata* Hamlin; Blanckenhorn: 125 (*non* Hamlin 1884).

Type material. According to Blanckenhorn (1927) the original specimen was in the collection of Professor Fraas in Stuttgart; this has not been verified. Mennessier (1984: 27; pl. 3, figs 42–45) quoted Hamlin's original figure as the holotype of *bicarinata* (Hamlin), and figured a 'neotype' from the Gollmer Collection in the Fac. Sci. Lyon and a 'paraneotype' in the Heybrook Collection, Univ. Paris VI.

Other material. In BM(NH): G.19465 (1), G.19472 (1), both from Beuah, Lebanon; Fahid collection purchased from Rev. C. Gollmer, 1907.

In Lyon: un-numbered specimen from Abeih, Lebanon, in Gollmer Collection (? this was given as the neotype of *M. bicarinata* by Mennessier).

Horizon & locality. In addition to the localities quoted above, Blanckenhorn (1890) and Delpey (1940) recorded *Paraglauconia frechi* from the Aptian 'oberer Trigoniensandstein' of the Lebanon at Abeih.

Other material of *Mesoglauconia*

Mesoglauconia frechi seems to be one member of a plexus of nominal species, listed below. Unfortunately the available material does not permit us to revise these taxa here: see Discussion (p. 274).

Further material from the Lebanon has been identified as follows.
Mesoglauconia ? frechi (Blanckenhorn). BM(NH): G.19481 (1) from Kielay; Fahid coll'n purchased from Rev. C. Gollmer, 1907. Fig. 15.1–2.
Mesoglauconia cf. *subseetzeni* (Blanckenhorn, 1927). BM(NH): G.19485 (1) from Kielay; G.17264 (3) and G.19495 (1) from Duccan; all part of the Fahid coll'n purchased from Rev. C. Gollmer, 1907. 83696 (2) from 'Olive' locality near Abeih, purchased from R. Damon, 1878.
Mesoglauconia cf. *renevieri* (Coquand). See p. 271 above.
Mesoglauconia bicarinata (Hamlin, 1884). BM(NH): GG.14377–8 (*ex* 83696) from 'Olive' locality near Abeih, purchased from R. Damon, 1878. Fig. 15.4.

Further material from Spain has been identified as follows; note that it is possible the original series of specimens figured by Vilanova (1863: 98; pl. 4, fig. 16 ('var.'); pl. 5, figs 18, 20, 22) as *Vycaria studeri* belong to more than one species.
Mesoglauconia cf. *renevieri* (Coquand). See p. 271 above.
Mesoglauconia cf. *studeri* (Vilanova). BM(NH): GG.21556 (*ex* 46029) from Benural (Teruel), purchased from M. J. Rothschild, 1864; GG.21558 (*ex* 70208) from Mirambel, presented by Prof. J. Vilanova, August 1869.
Mesoglauconia studeri (Vilanova), var. BM(NH): GG.21557 (*ex* 46029) from Benural (Teruel), purchased from M. J. Rothschild, 1864; n.b. this has preservation different from that of the other specimen (above) from this locality; 70208 from Mirambel, presented by Prof. J. Vilanova, August 1869.

DISCUSSION. In order to understand the relationship of the British species of *Mesoglauconia* we have examined specimens of other species from the Lebanon, Spain and Japan. However, we do not consider that a revision of these taxa should be made here, as we have insufficient material available. On the other hand it has been necessary to make particular interpretations and our observations are recorded as a contribution to any future revision of the genus.

We have not treated *bicarinata* and *frechi* as being synonymous as suggested by Mennessier (1984). It should be noted that if our interpretation of *Eunema ? bicarinata*, *sensu* Hamlin, is correct, then it is a junior secondary homonym of *Melania bicarinata* Dunker and would not be available in Hamlin's sense for a species of *Paraglauconia*. Our examination of material from the Lebanon suggests that existing nomenclature of the Middle East cassiopids does not reflect their variation in shell morphology. There is a need for a revision combining the shell characters noted above with more precise information on their stratigraphical occurrence.

Ecology of the Cassiopidae

The majority of previous interpretations have been influenced by the alleged occurrence of cassiopids in fresh-water and brackish deposits. Such a view stems, in part, from the fact that their oldest known European representatives, *Paraglauconia carbonaria* (Roemer) and ?*'Paraglauconia'* cf. *fittoni* (see Fig. 13.1) are found in early Cretaceous deposits which were thought to be non-marine. Stoliczka (1865) advocated the idea that most species of *'Glauconia'* appeared to be inhabitants of brackish or fresh water, and in common with him many subsequent authors (e.g. Mazeran 1911, Repelin 1902 and Douvillé 1921) have described such occurrences. Several have believed that the form of the shell and aperture were reminiscent of other gastropods restricted to such environments. They have also considered that the variation in shell form and ornament that occurred was another typical trait, possibly arising from comparative isolation in these environments. Pchelintsev (1953) believed that the majority of cassiopids had lived in fresh water, or in brackish habitats after becoming adapted to them, and that certain cassiopid taxa had later returned to their original marine environment.

Up to the present, there is no definite evidence for particular cassiopid species being stenohaline. Nor can we give a certain answer to Arkell's original question whether any single species was known to be euryhaline. We have only noted that various forms of a particular species may become more frequent at certain localities or in different formations, e.g. the Austrian *Cassiope kefersteinii* (see p. 247).

Andrews (1971, 1977) referred to the factors controlling the molluscs of in-shore habitats; in particular she stressed salinity and temperature. Although the inhabitants of estuarine waters are more adaptable and tolerant of fluctuations, rapid changes, especially of salinity, will interfere with their osmotic processes and disrupt cell tissues, with bivalves being the most vulnerable to such changes. It is the extremes that are the limiting biotic factors, especially if they last for some time. Consequently, we feel that the schemes of salinity zones used to classify estuarine and brackish waters are an over-simplification of both past and present situations (Tomlinson 1986: 21).

Most of the material available to us, i.e. from the Crackers (Isle of Wight), Teruel (Spain) and localities near Abeih (Lebanon), has been associated with marine faunas. It is also assumed that the cassiopids present in the Wealden associations described by Morter (1978: 21, 1984) are related to marine incursions. Kennedy & Macdougal (1969) have summarized the marked evidence for marine conditions in the Lower Cretaceous Weald Clay, and inferred that the occurrences of the crustacean trace fossil *Ophiomorpha* indicated an in-shore environment at the time the burrows originated. Allen *et al.* (1973: 615, 619) attested that the periodic marine incursions had been more frequent during Weald Clay times than earlier in the Lower Cretaceous. Elsewhere, we have suggested (Cleevely *et al.* 1984) that the environment represented by the Punfield Marine Band fauna, a deposit that has the most noteworthy occurrence of cassiopids in Britain, may have been estuarine. This conclusion is supported by the work of Day

(1981: 147) on modern estuarine faunas, who stated that most of the species present are marine in origin. Simpson (1983) also concluded that the decapod Crustacea and associated fauna of the Punfield Marine Band indicated marine conditions. The studies on Cretaceous faunas of Japan by Kase (1984: 119) also confirm that cassiopid-associated taxa are from marginal marine environments.

Fürsich & Kirkland (1986) have described a Cenomanian (Dakota Formation, northern Arizona) occurrence of a cassiopid in one of the four low-diversity faunules found in sediments deposited in what they interpret as a 'brackish lagoon'. *Gymnentome* (*Craginia*) *coalvillensis* (Stephenson) is one of the few faunal elements to reach normal size. In some samples, lenses of individuals formed the dominant element, attaining a relative abundance of 74%. These concentrations are thought to be populations, reworked *in situ*, of gregarious cassiopids that had formed a patchy distribution on the lagoonal floor. The authors considered that the salinity of the sediments in which they occurred was in 'the mesohaline to lower brachyhaline range' (5–20%).

In their explanatory environmental model Fürsich & Kirkland (1986: 558) considered that a barrier-bar coastline had prevented the establishment of fully marine conditions, but had led to the formation of an extensive lagoonal system. The salinity values had varied through influxes of fresh water and marine incursions, allowing the existence of several low-diversity faunal subsets. Whilst accepting their interpretation, we would consider that modern equivalent situations are even more complex and that both daily and seasonal alternations are a significant factor controlling faunal composition, producing frequent changes.

During the two relatively short periods of the Cretaceous that we have studied there is evidence of several distinct cassiopid morphologies. We interpret these as separate taxa living in habitats that range from marine in-shore, to backshore swamps and lagoons, to areas of water that may have had reduced salinities. One study involved the late Barremian to early Aptian occurrences of southern England; the other examined the Coniacian–Santonian records in Austria. The only evidence which suggests a fresh-water environment is provided by a species, which we have questionably referred to *P. fittoni*, that occurs in association with Unionidae from an unknown, possibly Lower Cretaceous locality in the Hannover Basin (see Fig. 13.1).

Various authors, Schenk (1971), Herm (1977) and Herm *et al.* (1979), have indicated that salinity is a significant controlling factor in the distribution of the cassiopid species occurring in the Gosau Beds of the Brandenburg area. It is apparent from the quite different cassiopid shell morphologies that each is part of a different faunal association. However, it is still difficult to establish the species present in the complex of cassiopids occurring in the Gosau Beds throughout central Europe. Akopyan (1976) showed that some of these species also occur widely along Tethys and extend into the Caucasus.

Herm (1977) has described the sequence of faunal associations found in the transgressive and regressive cycles of the Upper Cretaceous Gosau Beds of Brandenberg in Tyrol, Austria. Cassiopids occur in two of the fossil assemblages he has assigned to particular biofacies; the cassiopids were considered to be of minor importance in the *Radiolites–Trochactaeon* 'second' phase, but formed a significant element in his 'fourth' phase, the highly diverse *Polymesoda–'Glauconia'* assemblage. He considered that such molluscs were typical of brackish water environments (e.g. Schenk 1969, 1971). Kollmann (1984: 60) has also stated that these *Cassiope* lived in waters of reduced salinity, while acknowledging that they may be associated with the undoubtedly marine Naticidae. These authors utilize the salinity zones schemes, which after field observation of similar environments existing at the present time in south-east Asia (N.J.M.), we feel are too artificial and do not reflect the fluctuations of natural conditions.

A clearer understanding of the more typical Pan-Tethyan in-shore, shallow water environments preserved in these eastern Alps Cretaceous faunas can be obtained from Höfling (1985). From his detailed palaeoecological studies he recognized a number of varying environments. In particular, Höfling found that the cassiopids occurred in the fauna of the back-reef lagoons of the localized hippuritid rudist reefs, whenever these lagoons had remained marine. Observations (N.J.M.) at these and other localities in Austria indicated that the cassiopid habitats were clearly not off-shore.

Occurrences in Austria

We believe that there is a relatively simple distribution pattern among the cassiopids present in the Gosau Beds, but suspect that it may hide undetected subtleties. The pattern can be inferred from the number and types of species with which cassiopids are associated and the lithological nature of the sediment. In the more landward, and on average less saline, environment, where they are associated with ? Corbiculidae [= *Polymesoda* of Herm], *Terebraliopsis* and *Pyrgulifera*, we have *Cassiope bicostata* and possible representatives of *C. suffarcinata* (seen at Zöttbachalm, Brandenburg). In some areas west of Lake Balaton (Hungary), *Pyrgulifera* occurs without *Terebraliopsis* or *Cassiope*, and the same association has been described at Zöttbach (Herm 1977). In more seaward environments, *Cassiope suffarcinata* occurs with Naticidae and *Uchauxia* in a fine silty mud, which we consider represents a back-reef, or back-shore lagoon that may not always have been euhaline; this is seen at exposures on the north side of the river at Noth, to the east of Gams, near Heiflau (Styria). In the past, *C. suffarcinata* has also been commonly collected in the neighbourhood of Gosau, while in the Brandenburg area it may occur with *C. bicostata*. At Lanzing, to the north-west of Neustadt, *Cassiope lanzingensis* and *Uchauxia* occur in a bank of eroded nerineid shells (= *Helicoceras* sp.). This is also apparently to the landward side of a rudist patch reef containing subordinate corals, Nerinacea and Actaeonellidae. Above this rudist aggregate, *C. kefersteinii* is found; this species also occurs at Dreistetten, where it is associated with a wide variety of near-shore marine gastropods; badly preserved examples of *C. kefersteinii* are also found in the lower part of the marine sequence at Atzl Graben, near Brandenburg, below an actaeonellid-rich lime sand.

A much larger cassiopid, ? *Gymnentome gamsensis*, is occasionally found in a sandstone rich in *Acteonella lamarcki* and the nerineid *Helicoceras* sp., with rare *Pholadomya* sp. in life position, which we take to be fully marine in-shore sandbanks. Field data regarding *G. giebeli*, which may be synonymous with *G. gamsensis*, is not available.

In summary, therefore, we can make the following tentative interpretation of the spatial relationship of cassiopid species in the Upper Cretaceous of Austria: see Table 2 below.

a. Backshore lagoon, of lowered but variable salinity: *C. bicostata*, possibly *C. suffarcinata*.
b. Eulittoral backreef: *C. suffarcinata*, *C. lanzingensis*.
c. Eulittoral to sublittoral: *C. kefersteinii*, *G. gamsensis*.

Table 2 Spatial relationship of cassiopids in the Austrian Upper Cretaceous.

Backshore lagoon lower but variable salinity	Eulittoral backreef	Eulittoral—sublittoral
	Cassiope lanzingensis	*Cassiope kefersteinii*
Cassiope bicostata		
? ←	← *Cassiope suffarcinata*	*Gymnentome gamsensis*

Occurrences in England

In the Berriasian of northern Europe, *Paraglauconia carbonaria* is found in what appear, at first sight, to be monospecific shell beds, but which also contain very small smooth gastropods (possibly hydrobiids) and ostracods. This occurrence appears to be more inshore than the contemporaneous occurrences in England of *P. tricarinata*, either associated with the bivalve *Neomiodon* in the Weald or in the Corbula Bed fauna of the Swanage area. The paucity of species in these Wealden faunas must indicate an unusual, probably very variable, salinity, although there is no definite association with fresh-water species such as unionaceans or Viviparidae. The Corbula Bed fauna of corbulids, *Procerithium* etc. has to be interpreted as restricted marine with a similar non-standard sea-water salinity.

Paraglauconia fittoni occurs with a severely restricted number of species in the upper part of the Weald Clay. In the Late Barremian to early Aptian of southern England, *Gymnentome pizcuetana* is found in the fully marine fauna of the Crackers. This species is also found in the more marginal, probably estuarine, Punfield Marine Band along with *Mesoglauconia renevieri* and *Paraglauconia lujani*. This fauna has a vast array of marginal marine and marine species (Cleevely *et al.* 1984).

These occurrences, together with those in northern Europe at the same period and the Late Jurassic shallow marine specimens of *Paraglauconia* from the Arabian peninsula, suggest that by the beginning of the Cretaceous the cassiopids inhabited marginal marine and back-shore, but not fresh-water, environments.

In summary, we see the following generalized spatial relationship of cassiopid species in the British Aptian: this may be compared with that for the Upper Cretaceous of Austria on p. 276. See Table 3 below.

a. Backshore, not euhaline: *P. fittoni.*
b. Inshore marine or estuarine: *P. lujani, M. renevieri,* possibly *G. pizcuetana.*
c. Shallow marine: *G. pizcuetana.*

Table 3 Spatial relationships of cassiopids in the British Aptian.

Backshore not euhaline	Inshore marine or estuarine	Shallow marine
	Paraglauconia lujani	
Paraglauconia fittoni	*Mesoglauconia renevieri*	
	? ←	*Gymnentome pizcuetana*

Other evidence on the ecology of the Cassiopidae

Further support for the marine environment is given by the evidence of a moderately well preserved protoconch obtained from a specimen of *Paraglauconia tricarinata* (GSM no 26) which shows that species to have had a planktonic and therefore a marine larval shell (Fig. 19.1–2). The several stages preserved have been interpreted as firstly a smooth globose shell developed in the egg; followed by a free-swimming veliger stage of two whorls showing growth lines with an intervelar beak. The latter contrasts markedly with the more regularly-shaped growth lines occurring on the definitive post-metamorphic shell displaying some ornament. The procerithiid *Nerineopsis subattenuatum* (d'Orbigny) shows a similar series of growth stages (Fig. 19.3).

This protoconch is quite different from the bulbous embryonic shell of a few whorls that Houbrick (1984: 8) has described for some *Cerithidea*, which he regarded as typical of amphibious prosobranchs with direct development (1984: 13). The present fossil protoconch is comparable to that of *Cerithidiopsilla*, which is intertidal. Houbrick (1973, 1974) has also demonstrated that both 'indirect' and 'direct' modes of development occur in the genus *Cerithium*, and that the growth in the embryonic shell of the subtidal prosobranch *Diastoma melanioides* (Diastomatidae) is also direct (Houbrick 1981: fig. 1.I).

However, several specimens of *Paraglauconia lujani* from Utrillas (Teruel, Spain), in the École des Mines collection (at present in Lyon), were found to have been encrusted with bryozoans having structures now found only in taxa that inhabit brackish water (P. D. Taylor personal communication; Taylor 1986). Unfortunately, there is no direct evidence as to the precise horizons at which this species occurs in Spain; the literature merely suggests that it is associated with lignitiferous deposits (Coquand 1865, Aguilar *et al.* 1971). Mennessier (1984: 103) has argued that lignitiferous deposits might indicate the proximity of a mangrove environment

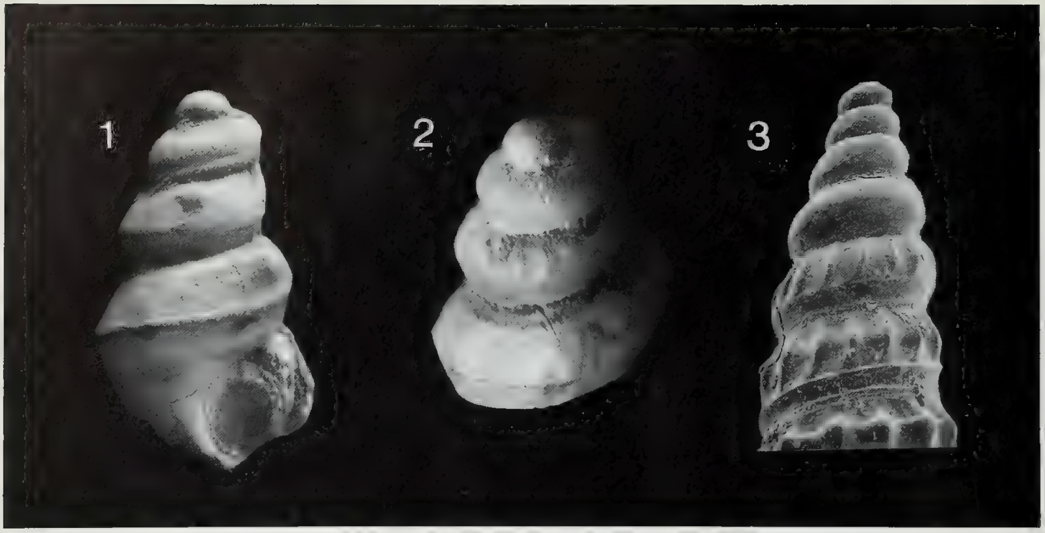

Fig. 19 Illustrations of protoconchs. **1, 2,** protoconch of *Paraglauconia tricarinata* (J. de C. Sowerby, 1836), from Purbeck, Greys Lst.; Burwash Wheel, nr Hastings; purchd H. Butler 1884. BGS GSM no. 26; electron micrograph ×88, showing several stages of shell growth: (i) a smooth globose shell developed in the egg; (ii) a free-swimming veliger stage with two whorls showing growth lines that extend into an intervelar beak; this contrasts markedly with the fourth whorl that is (iii) the post-metamorphic shell containing some ornament and more regularly-shaped growth lines. **3,** protoconch of *Nerineopsis subattenuatum* (d'Orbigny, 1850), from Lower Aptian, Crackers Bed, Atherfield, Isle of Wight; M. Durkin colln. BMNH GG.21498; electron micrograph ×50 approx., showing similar stages of shell growth.

('mangal', see p. 279), but there is no evidence of such plants. The various suggestions as to the existence of mangals in the Lower Cretaceous has prompted a number of botanists to consider the question; e.g. Hughes (1975: 451). The latter, after admitting 'most botanists have been reluctant to accept Mesozoic conifers—the only dominant lowland plant of that time—as occupying such sites', acknowledged that not all earlier conifers would necessarily have had the same ecological requirements as their more typical living descendants. Some support for this view has since been provided by the discovery in Australia of a conifer growing in a situation which is a modern analogue of the palaeoecological interpretation of the Upper Jurassic fossil 'forests' in Dorset (Francis 1984: 303).

Using plant fossils to reconstruct Wealden palaeoecology Batten (1974: figs 6, 7) has interpreted the early Cretaceous deposits as being part of a delta complex, with the clay formations representing transgressions and the sand formations the regressions. He concluded that the flora at that time was more influenced by sedimentary facies than present-day plants are. Amongst the speculative models Batten presented was the formation during the transgressions of coastal mangal by some members of the extinct *Hirmerella* group of conifers that produced *Classopollis* pollen. It has also been suggested (see p. 279) that the fern *Weichselia*, which occurs in the Hauterivian Horsham flora, might also have lived in a mangal habitat.

In his sketch of Mesozoic vegetation, Krassilov (1981: 212) mentioned the occurrence of a *Ptilophyllum* (*Otozamites*)–*Pachypteris* 'mangrove' in a 'warm' climatic Zone, a term he used in preference to the more contentious 'tropical' and 'sub-tropical'. He suggested that such 'mangroves' were also present, but less widespread, in an ecotonal 'warm-temperate' Zone, but that these 'mangrove' Bennettiales were not present in the temperate Zone. It is interesting to note that in his figures showing the distribution of these climatic zones during the Cretaceous, the boundary of his 'warm' Zone is well above the northern limit of cassiopid distribution during that period.

The Mangrove Ecosystem

Before any serious interpretation of the ecological habitat occupied by the cassiopids can be made, it is necessary to understand something of the present complex mangrove ecosystem. Full details are given by Chapman (1976, 1977) and other references.

MacNae (1968) proposed the term 'mangal' for the community, leaving the use of 'mangrove' for the constituent plant species. Mangal is strongly influenced by tides and typically extends along the sheltered estuaries of large rivers (Tomlinson 1986: 5) and in lagoons, but can also penetrate inland along river banks. Although it forms a discrete community, there is a close physiographic relationship with other strand communities and neighbouring elements often become intermixed. The mangal represents an interphase between the terrestrial and marine littoral ecosystems; often there is an abrupt transition from mangal to marine communities, but the change between mangal and terrestrial communities can be very gradual. The habitat has a high salt content and a high water content; its soils have a low oxygen content and abundant hydrogen sulphide (MacNae 1968: 121).

Mangal reaches its optimum development in the tropics, but extends into those regions forming part of the warm temperate belt wherever seasonal air temperature ranges permit (Chapman 1977: 1). Berry (1972) has summarized their essential and distinctive features and stated (1972: 156) that the many different habitats within the mangrove swamp/forest each supported a distinct animal community; he described six general zones. Chapman (1977: 18) also recognized these six mangal habitats but considered that the general ecosystem could be divided into distinct zoogeographical regions; others have shown that such zonation is modified, or elaborated to a mosaic (see Tomlinson, 1986: 16), according to topography.

A distinctive character of mangal is its diversity, and the resulting complexity has been summarized by Lugo (1980). MacNae (1968) distinguished the diverse animal microhabitats found in this environment, dividing them into infaunal burrowing and epifaunal errant, or wandering, forms. There are also two distinct modes of zonation: vertical zonation amongst tree-dwelling animals (e.g. *Cerithidea* species) and horizontal zonation for those living in the substratum. In the latter, MacNae records various molluscs associated with the landward fringe (1968: 174), the *Bruguiera* forests and *Ceriops* thickets (: 176–7), and the seaward fringes and channel banks (: 180). He notes that only *Telescopium* is present on the muddy floor of the *Rhizophora* forest, and describes the specializations shown by these marine mollusca (: 218): the majority are either grazers of the algae and micro-organisms living on the vegetation, or browsers on the organic deposits and their associated micro-organisms.

Other ecological evidence for molluscs in such habitats has to be gleaned from comments made in particular studies. Chapman (1976) states that the gastropods *Cerithidea* and *Melampus* were only found at the higher levels; Hutchings & Recher (1974) noted 16 species of Mollusca in a New South Wales fauna, with a maximum recorded density of 1,690 per m^2. Saenger *et al.* (*in* Chapman, 1977: 307), dealing with mangal communities in Australasia, pointed out the intertidal molluscs were exclusively either on trees or on the mud. They provided an extensive list (: 321–4) of 95 species of Mollusca, which included five species of Potamididae and seven of *Cerithidea*, most of which could occur together at some localities. Reimold (*in* Chapman, 1977), in a paper on the mangal habitat in eastern North America, expressed the belief that certain species of Mollusca were directly linked to the occurrence of particular plants. It has been pointed out (Tomlinson 1986: 10) that these faunal lists for mangal are long because both terrestrial and marine elements need to be included; this would also seem to explain and underline our own view of the mixed nature of the faunas in which the Lower Cretaceous cassiopids occur.

Finally, mention must be made of Chapman's (1977: 21) considerations on the evolutionary routes of mangrove plant species, divided into the two groups of Old and New World forms, in which he tentatively suggested that they began at the end of the Cretaceous and may have originated in a region of the Far East. Tomlinson (1986: 48) considered that this bimodal distribution is explained by an origin 'somewhere in the cradle of early angiosperm diversification'. He also refers to the view (Retallack & Dilcher 1981) that the fern *Weichsella* may have formed a pan-tropical mangal in the early Cretaceous, but feels that this could only have been equivalent to 'back-mangal' in today's terms.

Although the evidence available at present indicates that no mangrove species, or any other angiosperm, existed in Britain during this early period of the Lower Cretaceous (Hughes 1977, Muller 1981, Doyle & Hickey 1976, Hickey & Doyle 1977), Wealden palaeogeography certainly provided suitable conditions for them. However, *Nipa* is first recorded in the Maastrichtian, but the earliest record of angiosperm pollen is from the Brook, Isle of Wight, Barremian flora. As Chapman (1977: 2) remarked, 'the shallower and more extensive the shallows, the greater the extent of wet coastal formations'. Since the likelihood of true mangrove ecosystems in the Cretaceous is so remote, we prefer to adopt Chapman's term 'wet coastal ecosystems' to include the environments occupied by the cassiopids; this allows for distribution in tropical, sub-tropical, and perhaps even warm temperate belts.

Comparison with Recent Gastropoda

Inevitably we are compelled to compare the Cassiopidae with the Recent family of intertidal gastropods, the Potamididae, representing a similar estuarine radiation of the Cerithiacea. These are conspicuous inhabitants of the mangroves, salt marshes, muddy tidal creeks and estuaries of marginal tropical and sub-tropical regions. In a recent study of the comparative morphology of the genus *Cerithidea* (Potamidinae), Houbrick (1984) has made a number of observations concerning their habitat which could also apply to that of the cassiopids. Each of the different subgenera of *Cerithidea* appears to have its own general habitat within the intertidal zone: *Cerithidea* s.str. is essentially a tree-dwelling or tree-associated group, *Cerithideopsilla* lives mainly on muddy sandy substrates, while *Cerithideopsis* is a supratidal group living at the high-tide mark.

An alternative intertidal zonation distribution pattern, in which other potamidids occur, has been described by Morton & Morton (1983). Similar niche partitioning could account for the presence of several cassiopids in the same Cretaceous fauna, e.g. the Punfield Marine band.

Houbrick (1984) discovered that the Caribbean *Cerithidea scalariformis* Say had a marked sexual dimorphism in shell size; that an extended spawning period produced several cohorts of juveniles; and that the species had a wide tolerance of temperature, salinity and desiccation. The adults were amphibious and seldom in water, whilst the juveniles tended to remain immersed amongst the detritus of the creeks. In other species, in which adults congregate on the trunks of mangroves, descent is associated with feeding and tides. We feel that similar behavioural characters could account for the uniformity and range of variation exhibited in the shell morphology of different cassiopid fossil populations.

In an ecological study Egonmwan (1986) observed that the west African *Tympanotonos fuscatus* (L.) (Cerithiacea, Potamididae) migrated to the edges of the water and congregated under grass tufts or the pneumatophore roots of the mangroves; it was never found in the main body of the lagoon. During the dry season, it burrowed into the mud. The species favoured quiet waters with a muddy substratum rich in detritus and apparently adopted an 'amphibious' mode of life with the anterior part of the shell kept out of the water.

Houbrick also noted (1984: 8) that poor larval dispersal accounted for the patchy distribution and narrow geographical ranges of certain species of *Cerithidea*. Whilst this might explain and support the proliferation of fossil species described on the basis of geographical occurrence, such a trait would have prevented the Cassiopidae from using migratory routes open to other species. The confusion in distinguishing cassiopid taxa on the basis of their shell morphology might also be explained by his observation that the potential for the convergence of shell characters was quite high, since the same mode of existence was likely to have been adopted by several different clades.

Remarks on Palaeogeographical and Stratigraphical distribution

We have explained above that the majority of cassiopids occur principally in estuarine or intertidal environments. Mennessier (1984) summarized over 130 deposits with faunas that contained cassiopids and concluded that the majority were undoubtedly marine. However, although his observation that they are more frequently found in argillaceous environments is

basically true, his explanation that the cassiopids were adapted to deoxygenated conditions appears to be mistaken.

European palaeogeography in much of the Lower Cretaceous was a series of numerous large and small land masses, together with inland seas, situated between three large continental land blocks (see Neale, 1973: fig. 1). The seas had clear Tethyan and proto-Atlantic oceanic connections, now known from geological exploration for oil on the continental shelf to the west of Britain and off-shore from the eastern seaboard of North America.

From various accounts of the British Purbeck (Francis 1984), Wealden (Allen 1975, Sladen 1983) and Aptian (Casey 1961, Cleevely *et al.* 1984), it is apparent that suitable habitats for cassiopids existed around the coastal plain. Other general studies, assessing climatically significant criteria affecting the distribution of organisms, confirm that the more humid climate prevailing during these periods would have enabled these Tethyan gastropods to have extended their range 'northwards' (Barron 1983, Hallam 1984, Creber & Chaloner 1985). This climatic change had considerable effect on facies distribution and in particular the 'Wealden-type' siliclastics, which extended over a huge area of the northern hemisphere (Hallam 1984: 212), an area that coincided with the distribution of the cassiopids at that time.

Several authors have discussed the difficulties in correlating the Tethyan and Boreal realms of the Lower Cretaceous (Birkelund *et al.* 1984: 3–4; Kelly 1984: 3). Similarly, the many problems in exact correlation at the Jurassic–Cretaceous boundary have been fully dealt with by Norris (1985), who suggested a sequence of environments, inferred from palynostratigraphic considerations, that might have occurred in Dorset and the northern Weald at these times. However, since we consider that the molluscs known to occur in the critical Purbeck beds do not belong to the Boreal realm, but have strong Tethyan affinities, we intend to use the more appropriate term Berriasian when referring to their age. The presence of the facies-controlled, essentially Tethyan, Cassiopidae suggests that their occurrences may indicate areas where the different 'realms' recognized by other authors in the Lower Cretaceous, e.g. for Ammonoidea (Rawson 1973, Owen 1973) or for Brachiopoda (Middlemiss 1979), may have overlapped.

Examination of cassiopid distribution shows that the Berriasian *P. carbonaria* (occurring in the NW German Basin) and *P. tricarinata* (of the British Wealden) are amongst the earliest known Cretaceous records. The precise age of the species of *Paraglauconia* found in South America by Steinmann (1929) is not certain.

The early Cretaceous occurrences of cassiopids in northern Europe would seem to indicate marine connections with the Tethyan or tropical areas. The sedimentary basins that existed in Berriasian times were periodically invaded by the sea, presumably as a result of changes in sea-level. The direction from which these invasions came seems to us to be a matter of conjecture. Following the early Aptian transgression, the environments in which intertidal or supratidal Cerithiacea would have occurred are not found (or have not been preserved) in Britain again until after the end of the Cretaceous. It is interesting to note that *Cassiope* and *Craginia* both occur in a late Aptian benthic rudist community of southern Mexico (Alencaster 1984: 82). Such isolation may have led to the later development of different genera such as *Craginia* and *Cassiopella*.

The majority of cassiopid species recognized in southern Britain belong to *Paraglauconia*. It is suggested on p. 235 that these fossils can now be of some stratigraphical use within the British Wealden formations. The British records of Cassiopidae are significant for the following reasons. Firstly, they provide one of the earliest Cretaceous records of a cassiopid, *Paraglauconia tricarinata*; its Berriasian age suggests that it is contemporaneous with *P. carbonaria* occurring in the NW German Lower Saxonian Basin. Secondly, they would appear to include one of the richer fossil occurrences of this family in today's higher latitudes, with three species being present in the Aptian Punfield Marine Band at 50°N. Thirdly, apart from the German records at localities around Hannover at 53°N, at 50°–51°N they are the most 'northerly' occurrence of cassiopids. Smith *et al.* (1973: text-fig. 7) have suggested on palaeomagnetic evidence that the palaeolatitude of southern England during the mid-Cretaceous was approximately 35°Kr N (see Hughes, 1975: 450, text-fig. 2) and slightly less far north for the early Cretaceous; Hughes (1975: 449) has therefore concluded that the Wealden flora would have belonged to the palaeobotanist's 'southern province'.

Postscript (R.J.C., 5th March 1988).

Sohl (1987), in his important contribution on the faunal development and distribution of Cretaceous gastropods, has commented on the occurrence of the Cassiopidae. He confirms that gastropod assemblages were strongly controlled by salinity and substrate, but that their wider distribution was influenced by other factors such as current patterns. The boundaries between the biotic realms he recognizes had shifted with time, and he suggests that since all environments had been affected, temperature was the most likely control.

Sohl uses the distribution of the Cassiopidae to demonstrate that the filtering mechanism governing this intermixture of Tethyan and temperate taxa was primarily controlled by temperature rather than the presence of a suitable substrate (1987: 1094–5). He records the abundance of the family in both low-diversity brackish water and marginal marine assemblages, also suggesting that some might be 'river-mouth' assemblages. He notes that by the end of the Barremian, the Cassiopidae occurred from Peru eastwards throughout Europe to the Caucasus, and that following rapid diversification they spread through most of Tethys and its marginal regions, reaching their acme during Mid-Cretaceous times. He comments on their wide northern hemisphere latitudinal distribution, extending eastwards from North America across Europe to Japan. From the evidence available to him, Sohl concludes that their maximum northward extent coincided with the peak early Turonian transgressions (1987: 1095, fig. 5). Our own evidence, and that of both Mennessier and Akopyan, shows that the initial phase of Cassiopidae dispersal probably occurred in the Berriasian, somewhat earlier than Sohl suggested. From the apparent replacement after the Turonian of *Cassiope* by thiarid and melanatrid gastropods in suitable palaeoenvironments in parts of the northern hemisphere, Sohl argues that the warm-water assemblages to which they belonged had moved southwards. He believes this interpretation is partly confirmed by the occurrence of *Cassiope* and *Pyrgulifera* assemblages in only the Late Cretaceous deposits of Mexico and the Antillean Region. Incidentally, we are not aware of any precise evidence that establishes endemicity within the Cassiopidae.

Sohl (1987) divides Tethyan gastropods into three groups according to the times of their origin. He places the Cassiopidae in his Group 2, containing taxa originating in the early Cretaceous (1987: 1098, fig. 6; 1100, fig. 8.). Taxa in this group commonly show a wide latitudinal distribution, extending beyond the core of the framework-building coral and rudist Tethyan facies into marginal environments, and were often locally and numerically abundant. His summary of the development of the Cassiopidae conforms to the general pattern shown by that group: appearance in the early Cretaceous, rapid diversification and then decline after the mid-Cretaceous to eventual extinction at the end of the period.

This pattern is consistent with our own understanding, apart from its belief in the origin of the Cassiopidae in the Cretaceous. Their eventual demise was probably the result of the various factors he discusses. Although temperature control was undoubtedly a prime factor influencing their distribution, we consider that other alterations to their marginal environments, and even pure chance, may well have contributed to this decline, enabling other taxa to replace them in the various environments they had occupied.

Conclusions

Substantial progress has been made in recent years in understanding the history of the Cassiopidae, notably through the recognition that they are a distinct family (Pchelintsev 1953), the realisation that the position and shape of the growth lines was a generic diagnostic character (Akopyan 1976), and through the monographic compilation produced by Mennessier (1984). The latter attempted an overall assessment of the family and reiterated several observations on their evolutionary trends. In addition, he presented an analysis of their occurrence which largely affirmed their marine habitat rather than the brackish/non-marine habitat, which had previously been attributed to them.

Our study of British Cassiopidae from the Lower Cretaceous, augmented by investigation of Upper Cretaceous species from Austria and other material, suggests that the family had a marine origin in the Upper Jurassic (Tithonian) and persisted in essentially marine inshore/backshore environments, perhaps equivalent to estuarine (Punfield) or mangal-like (Wealden) situations, throughout this period. Their existence records an early invasion of such habitats by the Cerithiacea. In common with some present-day families of this superfamily, which occupy the same habitats, the Cassiopidae possibly had marine larvae.

The British Wealden and Aptian records would appear to be close to a northern limit of Cassiopidae distribution during these periods. Consequently, the environments they occupied are not directly comparable with the marine cycles occurring in their more tropical rudist-associated habitats preserved in the Gosau Beds of southern Europe.

Although this study has clarified the British occurrences and, it may be hoped, stabilized the nomenclature of several taxa in the family, considerable research is still required to establish and to understand fully their geological record and past history. There is still considerable scope for resolving the precise occurrence and distribution of members of the family in Cretaceous formations throughout the rest of the world. Records of their presence in Tethyan marginal environments are extensive. The scarcity of cassiopids in high latitudes together with their frequent association in facies associated with nerineids and rudists suggests that they are essentially 'Tethyan' and subtropical/tropical molluscs.

An accurate appraisal is limited by the nature of the wet-coastal environments that are occupied by the Cassiopidae, which are inevitably complex and restricted in occurrence. Consequently their preservation is limited and associated faunas seldom yield precise stratigraphical correlation. Similarly, the continual problem of determining aspects of cassiopid shell morphology presented by apparent variation within species contributes to our uncertainty. It appears from work by several authors on Recent families (Reid 1986, Vermeij 1974, Houbrick 1984) that some such differences probably reflect occupancy of different ecological niches. However, other changes arise in the normal course of an individual shell's development. In this paper, where noticeable changes in shell morphology can be associated with known and different stratigraphical horizons, we have recognized such cassiopids as different species, e.g. the Wealden species of *Paraglauconia*. On the other hand, where a considerable range of variation occurs at roughly the same geological horizon and intermediate forms exist, e.g. *Cassiope kefersteinii* and *Paraglauconia lujani*, we have accepted that they belong to a single variable species.

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Sadly we have to record the recent deaths of two pre-eminent workers on the Cassiopidae, Professor Guy Mennesier and Dr V. T. Akopyan, and regret the loss of any further contribution from their interest in the subject.

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